Conflict in Context: A critique and investigation into the logic, nature, and evolutionary consequences of competition in animals

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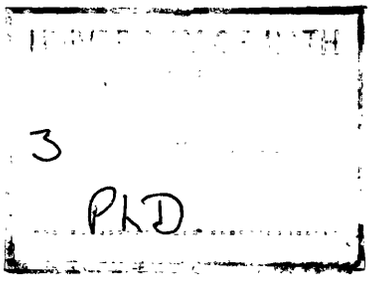
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Contents

Abstract

The conventional logic of competition assumes a general 'struggle' between organisms for access to food or mates. As a consequence of this 'struggle', it is suggested that the most vigorous and competitive individuals usually win out at the expense of their rivals. Despite the clear advantage certain individuals have over others, fitness gradients are maintained in all natural populations. I address this paradox using two complementary approaches. First, I address gender-biased assumptions embedded in traditional mate choice models, and critically examine the extent to which evolution is driven by male-male competition, which is assumed to favour the most vigorous males. I propose that such androcentric bias exposed by feminist critiques is a symptom of a larger problem posed by the conventional neo-Darwinian paradigm. Therefore, I address some of the problems associated with the conventional logic of competition, and propose an alternative perspective, which may help to dissolve the inconsistencies embedded in our current logic.

To complement my theoretical critiques, I explored intraspecific competition in three different animal taxa: Birds, insects, and mammals. My first objective was to investigate the effects of reproductive competition on male morphology and mating behaviour in bustards (Otididae). Then, in the American Rubyspot damselfly (*Hetaerina americana*), I explored how reproductive competition influences alternative mating behaviours in males. Finally, I used what has been considered an unusual animal, spotted hyenas (*Crocuta crocuta*), to expose the problem of rigid male-biased approaches to science, and how they have been responsible for mis-representing a number of animal groups including spotted hyenas. Then, I investigated various forms of competition and cooperation in the female dominance hierarchy with a special focus on the relationship between female social rank and the pattern of female coalition formations, and their evolutionary consequences in terms of female reproductive success and group dynamics. Finally, I integrate these studies into a coherent framework, which focuses on the active ways in which animals respond to and influence diverse contexts of competition.

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First of all I would like to thank my main supervisor, Professor Helen Haste, for providing me with the opportunity and support to conduct my PhD in the department of Psychology. Helen's passion for innovative and original works allowed me to explore my research interests using both conventional and non-conventional methods. I would also like to thank Dr. Alan Rayner, who offers a novel perspective, termed inclusionality, which questions the conventional logic of competition by including space as vital source of evolutionary creativity, in which life forms are "pulled together" as a result of their imperfection, rather than "pushed apart" in their strive towards perfection. This helped me to interpret the nature of competition in my study groups from very diverse perspectives. Dr. Tamás Székely, my undergraduate supervisor, inspired me to work in the field of animal behaviour, owing to his endless passion for the evolution and ecology of birds. Tamás's support and friendship throughout my postgraduate research has been of great importance from the beginning to the end of my thesis. I am also very grateful towards Dr. Marion East, who kindly offered to co-supervise my PhD. With her help I was able to study spotted hyenas in the wild, which would not have been possible without her support. I extend my gratitude to Alejandro Serrano-Meneses, who offered me the opportunity to work with the American rubyspot damselfly, in which I had the freedom to explore the types of behaviours that contributed to my overall research interests. Dr. Alejandro Córdoba-Aguilar also helped and supported my research interests in damselflies.

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Chapter 1: *A review and critique of the study of competition in animals*

Gina Raihani

My childhood dream, my lifelong wish, would have been fulfilled if it had really been possible to converse with animals.

Hediger, 1985

1. The logic of competition

1.1 Natural selection

The Darwinian and neo-Darwinian synthesis of natural and sexual selection

Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations, and the rejection of injurious variations, I call Natural Selection.

Darwin, 1859, p. 80-81

According to Darwin's (1859) theory of evolution, natural selection favours those organisms that are the most suited for survival. One example that contributed greatly to the formulation of Darwin's theory of evolution by natural selection was the phenotypic variation between the beaks of 13 species of Galápagos finches (Darwin, 1859). Darwin argued that Galápagos finches evolved diverse beak morphologies, since the beak of each species was suited to a highly specialised diet. Darwin recognised the importance of this variation, which promotes evolutionary change via natural selection. Recent work on beak morphology has also focused on the consequences of changes in beak size in Galápagos finches. In a series of studies Rosemary and Peter Grant (e.g. see review: Grant and Grant, 2003) demonstrated that diet and beak size are tightly associated and that slight variations in beak size affect survival, especially during periods of food

limitation. Although Darwin acknowledged the heritability of characters (although he was not familiar with Mendel's work on character inheritance in pea plants at the time), he was not able to understand the mechanisms and processes that generate variation. Thus, it was not until Watson and Crick (1953) proposed the specific structure for the genetic material that evolutionists were able to understand the mechanism of change at the level of the gene.

1.2 Sexual selection

According to Darwin and many current evolutionary biologists, natural selection is considered to be the main 'driving force' behind evolution, because only natural selection can discriminate between beneficial/adaptive and non-beneficial/non-adaptive genes, leading to the elimination of deleterious mutations (Muller, 1950). However, not all organisms conform so neatly to the principles of natural selection.

It is curious that I remember well the time when the thought of the eye made me cold all over, but I have got over this stage of the complaint, and now small trifling particulars of structure often make me very uncomfortable. The sight of a feather in a peacock's tail, whenever I gaze at it, it makes me sick! ...'

(Darwin, in Burkhardt *et al* 1993, p. 140)

Contrary to the predictions of natural selection, many animals develop exaggerated traits that appear to impair, rather than facilitate survival. Thus, how can natural selection alone explain the widespread differences between males and females in morphology and behaviour? In particular, Darwin noted that males were generally larger and stronger than females, and often exhibited weapons, extravagant ornaments and striking colours (Darwin, 1871). Fortunately, Darwin was able to find a plausible explanation for why such differences arise. Unlike natural selection, which is concerned with how organisms manage to survive in relation to others, '*sexual selection depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction*' (Darwin 1871, p. 256, vol. 1). Therefore, sexual selection appears to be more 'playful' and unpredictable in nature compared to natural selection, since it has resulted in a diversity of unusual traits and

behaviours in organisms that appear to be costly in terms of survival but highly beneficial in terms of reproductive success. From the perspective of Darwin, who was influenced by a particular era, sexual selection acted primarily on males:

'The sexual struggle is of two kinds: in the one it is between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; while in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners.'

Darwin, 1871, p. 398, vol. 2

Nowadays we divide sexual selection into two types of selective processes: intrasexual (male-male competition), and intersexual competition (female choice). In intrasexual competition one would expect males to evolve weapons, such as the modified pronotum of male stag beetles, which is used for fighting off rivals. In intersexual selection males display their ornaments, while females evaluate potential mates, allegedly using the information advertised by these ornaments (I talk about inter- and intrasexual selection in more detail in Chapter 3)

According to Darwin natural selection and sexual selection were opposing selective pressures, since the former aided survival, while the latter posed a threat to survival but enhanced reproductive success. Since Darwin proposed the theory of sexual selection, it has been firmly rejected by many biologists, including Alfred Russel Wallace, Thomas Hunt Morgan and Julian Huxley (see Hiraiwa-Hasegawa, 2000). Perhaps these initial tensions that existed between the theories of natural and sexual selection, contributed towards the separation of natural and sexual selection into discrete evolutionary processes. However, most evolutionary biologists nowadays view sexual selection as a component of natural selection, by viewing overall fitness as the sum of survivorship, fecundity and mating success (see Arnqvist and Rowe, 2005). Thus, although natural and sexual selection appear to act in opposite directions (Darwin, 1859, 1871), they do not necessarily result in a trade-off between promoting mating and threatening survival, since evolutionary adaptation depends on overall fitness, which is a product of both mating success and survival (Kodric-Brown and Brown, 1984).

1.3 Hypotheses of sexual selection

1.3.1 The Fisherian and handicap model of sexual selection, and the evolution of female choice.

One of the problems faced by evolutionary biologists is to find an explanation for the evolution of mate choice and in particular the origin of the female preference for males with seemingly maladaptive traits (Kirkpatrick and Ryan, 1991). Female choice, preferences or mating biases are characteristic of '*any female trait (behaviour, structure, etc.) that biases conspecific male mating/fertilisation success toward certain male phenotypes*' (Arnqvist and Rowe, 2005, p. 17). This broad definition of female choice is suitable for a wide range of taxa, since it does not imply that that 'choice' is necessarily a mental act.

One of the first major attempts to include the concept of female choice as an essential component of sexual selection was undertaken by R.A. Fisher (1930), who introduced the runaway process to explain the rapid evolution of a male trait and the female preference for the trait. Fisher (1930) suggested that the male trait and the female preference for the trait are correlated, which inevitably drives the coevolutionary exaggeration of both the trait and the preference. However, Fisher also stated that the "initial advantage", and therefore the origin of the preference, is not the preference itself, but rather the higher non-mating fitness of preferred males (see Arnqvist and Rowe, 2005). Also, it is considered that females that mate with 'sexy' males will produce offspring in which males inherit the genes for the preferred male trait ('sexy son' or Fisher process), while females inherit the preference for the male trait. However, female preferences can lead to the exaggeration of the male trait beyond its natural selection optimum. At this point the male trait becomes a hindrance to survivorship, and the evolution of the male trait and its correlated female preference become halted by natural selection.

This problem of the runaway process guided biologists to another aspect of Fisher's model, namely that attractiveness might be an indicator of viability and hence 'good genes' (Zahavi, 1975). This is also referred to as the handicap model, since Zahavi

argued that only the 'fittest' males could cope with the costs of expressing traits that appear to jeopardise survival. This resulted in a dichotomy between Fisherian runaway, presumably driven by the benefits of producing 'sexy sons', and the 'good genes' model, in which mate choice evolves because attractive males advertise longevity and fecundity (Kokko et al., 2003). Kokko et al. (2003) criticised this dichotomy, since 'good genes' that enable sons to achieve high mating success, are conceptually no different from genes that enhance offspring survival. However, it remains to be tested how these genes influence the life-history trade-off between survival and reproductive investment for offspring (Kokko et al., 2003). Lande's (1981) models showed that natural and sexual selection are balanced along a line of equilibria. Depending on the values of the trait and the preference, and the initial conditions, the population could reside at any point along the equilibrium line. Thus, Lande's models help to explain the evolution of sexual dimorphism and the huge variation among species in sexually selected traits.

One of the main problems regarding Fisherian and handicap models of sexual selection is the assumption that there is no direct selection on the female preference, since the Fisher runaway model and the good genes model rely on a tight association between the genes for the preference and those for the male trait, which is crucial for their coevolution (see Arnqvist and Rowe, 2005). For example, in these indirect models, the preference evolves only because they become genetically associated with the genes that result in sexy sons and/or high-viability offspring (Chapman et al., 2003). It is thought that these indirect processes play the most important role in the coevolution of the sexes, even when females benefit directly by receiving nuptial gifts and/or parental care from males (see Chapman et al., 2003).

Furthermore, the rate of evolution of the preference depends on its amount of genetic covariance with the male trait: if the genetic covariance is large enough, then the runaway of the trait and the preference can occur rapidly, in which case neither the male trait nor the preference reaches equilibrium. Contrary to Darwin's idea that sexual selection aids natural selection, sexual selection in the Fisher process leads to the male trait and hence the preference, diverging from their natural selection optimum (see Arnqvist and Rowe, 2005). Evidence that there is direct selection on the female preference is supported by studies that demonstrate a cost to female choice in terms of

energy, time and risk of predation (e.g. Reynolds and Gross, 1990). Here, the argument states that since female fecundity and viability are affected by mate choice, there should be direct selection on the preference. This diminishes the effect of the Fisher process on the equilibrium value of the preference and trait, since the female preference will fall at a value that is best for female viability and fecundity, rather than being dragged indirectly by the male trait. Conversely, the indicator model can account for the costs of female preference, since in this scenario the females benefit from the non-mating fitness advantages of the male trait. Therefore, the costs of the preference will become balanced with the indirect benefits of the preference, which can explain the costly exaggeration of the male trait by the female preference.

1.4 The Lek Paradox

Leks are aggregations of displaying males, which females visit solely for the purpose of mating. There is no apparent direct benefit of choice for females apart from 'good genes' for their offspring (Kirkpatrick and Ryan, 1991; Andersson, 1994). Directional selection on the male traits, via female choice, is expected to deplete additive genetic variance (genetic variance associated with average additive effects of alleles -- see Tomkins et al., 2004). Despite the tendency of selection to deplete variety, additive genetic variance in sexually and non-sexually selected traits is abundant in nature. In studies on sexual selection this has become known as the Lek paradox (Borgia, 1979; Taylor and Williams, 1982; Kirkpatrick and Ryan, 1991; Andersson, 1994): If females prefer certain male traits that indicate viability, then the increased mating success of males bearing them should rapidly exhaust genetic variation for viability and drive the traits to fixation such that the 'best' genotype predominates (Charlesworth, 1987). Also, the depletion of genetic variation would remove the benefits of choice. Despite these predictions, choice and genetic variability in males persists (Tomkins et al. 2004).

If a particular trait is under directional selection, then how is additive genetic variance maintained? Two hypotheses may be put forward. First, sexually selected traits are condition dependent (Rowe and Houle, 1996; Tomkins et al., 2004). This hypothesis depends on two critical premises: 1) sexually selected traits evolve condition-dependent expression, and 2) There is large genetic variance in overall condition. Therefore, sexually selected traits will express the high variance in condition (genic capture), since

it is assumed that condition is influenced by a large number of loci (Tomkins et al., 2004). As a consequence one would expect a higher frequency of mutations in genes that influence condition and maintain variation. However, the frequency of these mutations needs to be quantified for the full resolution of the lek paradox (Kotiaho et al., 2001). Second, it has been proposed that females occasionally make mistakes when choosing their mates (Neff, 2000). Therefore, this degree of error in mate choice maintains genetic variation. This hypothesis was supported by a model using the butterfly *Acraea encedon* (Randerson et al., 2000). This species exhibits sex-role-reversed leks, in which females display to choosy males. Sex-role-reversal in *Acraea encedon* is thought to be due to a male-killing bacterium, which is passed from mother to offspring in the egg. In the model, Randerson et al. (2000) introduced a mutant choice gene, which enables males to differentiate between infected and uninfected females. The results showed that despite the ability of mutant males to identify the bad gene, there was a degree of error in mate choice so that males did occasionally mate with infected females. Therefore, the choice genes as well as infected and uninfected females are maintained in the population (Neff, 2000). Nevertheless, these results do not exclude other possible explanations for why males mate with infected females, for instance life-history constraints in which 'choice' may be costly.

Another example of the diversity problem is the paradox of plankton (Hutchinson, 1961). According to the theory of competitive exclusion, the number of coexisting plankton should not exceed the amount of limiting resources (Gause,1934; Tilman et al., 1982). However, despite living in relatively unstructured environments and competing for similar types of resources, different species of plankton are able to coexist on limited numbers of resources. Huisman and Weissing (1999) attempted to solve this paradox by showing that multispecies competition generates the necessary competitive fluctuations that in turn create opportunities for coexistence. Therefore, they concluded that non-equilibrium dynamics generated by species interactions themselves are critical for the maintenance of biodiversity.

These paradoxes may be telling us something quite profound regarding the way we perceive and study competition in animals. The problem of competition, which I address later on in more detail, is what I term the confusion between 'fitness' and 'fittingness.' The former relies heavily on the assumption that the genotype is of

primary importance for the reproductive success of an organism. Therefore, competition should favour those individuals with the highest genetic quality. The problem with this model is that it often results in paradoxes regarding the coexistence of diversity in nature. I suggest that our conventional logic of competition is responsible, since it tends to deemphasise the primacy of the fit between organism and its ever-changing dynamic context. Thus, how can a single determinant of fitness (i.e. genes) enable animals to adapt to their changing circumstances? I show later on in the American rubyspot damselfly that males of less competitive ability can still successfully mate with females by adopting alternative mating strategies, which appear to be context-dependent rather than genetically determined. Therefore, competition may be important for the evolution and maintenance of diversity if organisms are able to respond to competition in different ways. If individual responses to competition endow them with at least some fitness benefits then fitness gradients can be maintained in populations (e.g. conditional mating tactics, see Gross, 1996). I propose that behavioural flexibility may be a critical factor that enables individuals to respond to diverse contexts and intensities of competition in a way that suits their individual, social and ecological circumstances. Since competition can potentially result in creative solutions and hence novel adaptations, behavioural flexibility may dissolve the paradoxes of diversity discussed so far. I return to this important point later on in the discussion and provide some examples.

In the next section, I stress the importance of alternative perspectives in the study of animal behaviour and evolution by describing the ways in which feminist critiques in biology have transformed many out-dated ideas embedded in conventional sexual selection theory. Feminist perspectives have benefited biology by exposing a multitude of gender-biased assumptions and inconsistencies in the animal behaviour literature, which often misrepresent the sexes (in particular the primate order) by prematurely adopting well-established assumptions regarding typical male and female sexual behaviour. I suggest that feminist critiques either directly or indirectly address the problem of definition-driven explanations of behaviour. This is also known as determinism, in which initial conditions are first defined and then everything else is interpreted in terms of the definition without ever questioning the definition itself. However, this frequently leads to paradoxes when trying to understand dynamic and context-dependent behaviours.

2. The rise of feminist perspectives in science and their impact on traditional views of males, females and sexual selection

Researchers across various disciplines frequently make assumptions about sexual behaviour based on whether an individual is male or female (Haste, 1993). Given some of the existing paradoxes that arise out of traditional mate choice models, it is important to explore alternative perspectives, in particular feminist approaches to animal behaviour, since they have exposed a number of inconsistencies in the animal behaviour literature. These inconsistencies arise when only partially true gender-biased assumptions become uncritically applied to a wide range of animal groups. An example of how science can be influenced by our cultural preconceptions of gender 'norms' is the study of mating systems in birds pioneered by David Lack (1968). Both Lack (1968) and Darwin (1871) considered the majority of birds to be monogamous (or socially monogamous; i.e. male-female pairs on territories). However, Lack and Darwin worked on birds in an era with a considerable limitation of the scientific tools available. Lack found that the majority of birds were monogamous (Lack, 1968). Only recently have we learned that behaviourally monogamous species have a large number of extra-pair copulations (see Birkhead and Moller, 1992,1998; Birkhead, 2000) so they are not monogamous in the strict sense. To truly understand the mating system of a given species molecular techniques were required. This example demonstrates that Lack's ideas fitted the ideas of that time (i.e. that monogamy was "normal"), since only hard evidence could convince the scientist that monogamy was not the norm (for a review on avian breeding systems see Ligon, 1999; Bennett and Owens, 2002).

Another good example in the debate on sex and gender has in particular raged in the primate world between those who see primate society hinging on male aggression and control (see Sperling, 1991), and those that see both aggression and affiliative behaviours as a tool for resource negotiation (Aureli and de Waal, 2000). Therefore, our understanding of any system largely depends on where we are coming from and the type of logic we use. For example, in spotted hyenas the complete lack of sexual dimorphism and the fact that female genitalia resembles that of the males, has led certain scientists to the conclusion that females are hyperaggressive, and this aggression is driven by abnormally high levels of male hormones found in females (Glickman et al., 1993). However, recent evidence contradicts the hyperaggressive androgenised

image of spotted hyenas, which is largely based upon unfounded assumptions rather than scientific evidence (East and Hofer, 2002).

In the 1970s, Sarah Blaffer Hrdy and other female primatologists challenged the popular view of male and female sexual stereotypes. In her chapter in '*Feminist approaches to science*' (Bleier, 1986), Hrdy challenged the assumption that females are always sexually passive and discriminating by demonstrating that many female primates actively manage their sexual relationships in a way that undermines the traditional notion of mate choice. However, before addressing these issues I describe the nature of these gender stereotypes, which stimulated new insights and perspectives from feminist scientists.

2.1 The Darwin-Bateman paradigm

By describing females as sexually "coy", Darwin's original ideas on sexual selection deemphasised the complexity of females and their sexual behaviour. In this scenario females are considered to discriminate between and mate with the most attractive males, which are typically eager and undiscriminating. In Lande's (1981) models it is assumed that selection acts directly on the male trait, while the female preference can evolve as a response to selection on genetically correlated male traits. The primary focus of selection acting on male sexual traits was reinforced in Bateman's experiments in *Drosophila* (Bateman, 1948) from which he concluded that 1) males exhibit more variance in reproductive success compared to females, 2) males gain more benefits from multiple matings, and 3) males are usually ardent while females are sexually coy (the Bateman paradigm, Hrdy, 1986).

Starting from these initial premises scientists have looked for the type of traits that would be favoured by sexual selection. Sexual selection is thought to influence male and female traits and behaviours when partners vary in their ability to provide genetic material and social benefits (Andersson, 1994). For example, if males are able to win contests over females or other resources and provide females with these valuable resources, then it is generally assumed that it is in the females' best interest to mate with the strongest and most dominant males (Andersson, 1994). Therefore, traits reflecting dominance such as large body size and signs of fighting ability (i.e. horns, antlers etc.)

are expected to influence female choice (see Qvarnström and Forsgren, 1998), since selection should favour those males with the most competitive ability. Thus, it is often predicted that large body size, fighting ability or aesthetic traits and courtship displays (Darwin, 1871; Kodric-Brown and Brown, 1984; Andersson, 1994; Andersson and Iwasa, 1996), and the ability for males to coerce or force females to copulate with them (Clutton-Brock and Parker, 1995) are important for males to gain mating opportunities.

However, it is not true in all species that females prefer to mate with the most dominant males, even when high status males are able to win contests against other males (Qvarnström and Forsgren, 1998). Also, it has been demonstrated that fitness is not always a function of size (e.g. in some odonates: Thomson and Fincke, 2002) or aggression (e.g. the lizard *Psammodromus algirus*: Civantos, 2002). For example, in the ovoviviparous cockroach, *Nauphoeta cinerea,* females actively avoid mating with manipulative males and live longer as a consequence (Moore et al., 2003).

The initial dichotomy between the active, sexually eager male and the sexually uninterested, choosy female is characteristic of the Victorian era in which Darwin lived (Hrdy, 1986). However, the dominance of this dichotomy has had a profound influence on Darwin's followers, which is epitomised by the anti-feminist writer, Robert Wright (1994), who states that feminists fail to acknowledge the scientific truth about human nature (see Fausto-Sterling et al., 1997). A move away from this dichotomy (though not entirely) is the relatively novel paradigm of sexual conflict, which focuses on the way females respond to male sexual behaviour, and vice versa.

2.2 Conflict between the sexes

Sexual conflict (Parker, 1979) is a new paradigm, which provides novel insights into sexual selection. Parker (1979) defined this conflict as a conflict between the evolutionary interests of males and females, and it has been theorised that sexual conflict could lead to rapid divergence within populations and speciation (Arnqvist et al., 2000; Gavrilets, 2000). Sexual conflict differs from sexual selection, since it can potentially create novel selective processes but is not the selective process itself (Parker, 2006). However, although the theory of sexual conflict is dynamic, in that it does not necessarily assume male-male competition and female choice, it does nevertheless rely

heavily on the assumption that anisogamy (unequal gametes) results in differential interests between males and females (e.g. in the context of parental care). For example in a review on sexual conflict, Chapman et al. (2003, p.41) stated that '*Males and females have divergent interests in reproduction that are rooted in anisogamy and lead to distinct roles, where traits favoured by one sex might be costly to the other*'.
However, in the context of parental investment, it has been argued that anisogamy alone does not account for differences in male and female parental investment patterns (Kokko and Jennions, 2003; Wade and Shuster, 2002; Queller, 1997; see next section).

2.2.1 Sexual conflict over parental care

Though not explicitly anti-feminist *per se*, other scientists followed in the footsteps of Darwin and Bateman, such as Robert Trivers, who expanded the Bateman paradigm in his 1972 essay on "*Parental Investment and Sexual Selection*" (Trivers, 1972). According to Trivers' formulation, the sex that invests the least in offspring (usually males) will compete more to mate with the investing sex (usually females). Also, it is generally assumed that males can produce unlimited amounts of sperm continuously, while females can produce only a limited amount of eggs throughout their lifespan (Fausto-Sterling et al., 1997). Trivers (1972) argued that anisogamy could explain male and female sexual behaviour and parental investment patterns. Since eggs are costly, females are predicted to invest more into their offspring compared to males, who benefit more by deserting their partner to seek more mates. Therefore, apart from the rare circumstances in which males invest more and females are the competitive sex, it is the females that will usually benefit from being monogamous and care for their young, while males are selected to be promiscuous and desert their partners (Tang-Martinez and Brandt Ryder, 2005).

Due to the substantial investment on the female side, females are thought to mate with the 'best' available male (Hrdy, 1986). Trivers also reinforced the ardent male-female coy hypothesis when he summarised Bateman's experiments (see Hrdy, 1986): "A female's reproductive success did not increase much, if any, after the first copulation and not at all after the second; most females were uninterested in copulating more than once or twice" (Trivers, 1972, p. 138). Interestingly, Trivers (1972) and others failed to

distinguish between Bateman's definition of a 'mate', and what most animal behaviourists define as a 'mate'. Bateman's use of word 'mate' only took into account the number of partners with which an individual successfully produced offspring. However, the proper use of the term 'mate' is a partner with which an animal pairs and/or copulates, which may or may not result in the production of offspring (Dewsbury, 2005). What Bateman in fact studied was *reproductive* success in relation to the number of partners, not the number of copulations or pairings per partner, since he only included the number of matings obtained by genetic markers carried by the progeny (Tang-Martinez and Brandt Ryder, 2005). Therefore, Bateman was not able to infer the number of mates, since he did not conduct any behavioural observations (Dewsbury, 2005).

However, in a series of experiments in *Drosophila pseudoobscura*, Turner and Anderson (1983) demonstrated that females benefited when they were allowed to mate with several males and for longer periods, since they produced a larger number of offspring that survived to maturity, compared to females that were only allowed to mate briefly with a single male. However, Bateman's finding that females can enhance their fertility by increasing their number of matings (Birkhead, 2000) was ignored for several decades following the publication of his data. Other possible benefits of mating with multiple males (see Birkhead, 2000; Jennions and Petrie, 2000) include 'the renewal of depleted sperm supplies, improvement of genetic quality and diversity of a female's offspring, increased access to resources, and increased lifetime offspring production' (Dewsbury, 2005, p. 834).

Also, the assumption that egg production is more costly than sperm production is often accepted without the support from convincing scientific data (Fausto-Sterling et al., 1997). Dewsbury (1982) reviewed the male costs of reproduction, such as sperm competition and female choice or control, and concluded that the view that males mate indiscriminately and with as many females as possible needs to be re-examined in the light of evidence for male ejaculation costs, factors that affect the allocation of ejaculates, and male mate choice. It has been demonstrated that sperm ejaculation can be expensive and that choice of mates is not always restricted to the female sex. For example, different species of *Drosophila* vary in sperm size, and it has been shown that those species that produce gigantic sperm (10 times male body length) experience

delayed maturity, which suggests that the production of large sperm is costly (Pitnick et al., 1995). Also, Dewsbury pointed out that male mate choice might be important when there are costs to ejaculation and sperm competition (Tang-Martinez and Brandt Ryder, 2005). The discovery of sperm competition by Geoffrey Parker in 1972, demonstrated that females mate with many different males, and that females can select amongst sperm from different males once in their reproductive tract (see Birkhead and Moller, 1993).

Many feminist Darwinists argue that female-male relationships are extremely dynamic and that the contexts of sex and rearing offspring are extremely variable, which can lead to environmentally contingent changes in their behaviours (Fausto-Sterling et al., 1997). Kokko and Jennions (2003) demonstrated that the idea that anisogamy should lead to females caring more for offspring compared to males is incomplete. Anisogamy has been used to explain why there is a taxonomic bias towards female parental care, rather than male parental care (Wade and Shuster, 2002). The argument states that since females produce large and costly eggs, while males produce small and cheap sperm, it is generally the female sex that will care for her offspring, since reproductive success in females is limited by the number of eggs she can produce, whereas in males reproductive success is determined by the number of females he can access and successfully mate with. Therefore, males can potentially gain more, in terms of fitness, from deserting their offspring compared to females. However, anisogamy alone does not predict male and female parental investment patterns. In a model, Queller (1997) showed that both the probability of male paternity and sexual selection can influence parental investment patterns. Queller (1997) argued that in populations with equal sex ratios, a bias towards female parental care is not necessarily rooted in anisogamy if the total numbers of males and females in a population have identical future prospects for reproduction. For example, if each male can only mate successfully with one female, and assuming that the costs of caring are equal for both sexes, one would expect equal investment in parental care by males and females. However, the costs and benefits of caring can become unequal between the sexes if some males are able to gain a higher proportion of matings at the expense of other males, either by being more attractive to females, or competitively superior in contests with other males. This results in some males in a population having a higher reproductive rate than females, which increases their relative fitness gain by deserting.

Also, when a female mates with more than one male, the probability of parentage for mated males decreases with the number of males the female mates with. Therefore, the benefits of caring for these males are lower compared to the female if males do not know which offspring they sired, and how many. Kokko and Jennions (2003) concluded that anisogamy sets the conditions for sexual selection, often leading to a bias towards female parental care.

In conclusion, male and female parental investment patterns show a tendency towards female-biased parental investment, due to differences in the relative male and female fitness payoffs regarding mate desertion. This appears to be driven by sexual selection, since a subset of males can potentially mate with several females at a cost to other males who may gain very little or no mating opportunities. Therefore, certain males may monopolise most matings even when the overall population sex ratio is 1:1. However, the proportion of male and female parental care is often context-dependent. For example, in the lesser spotted woodpecker (*Dendrocopos minor*), females are often polyandrous when the population sex ratio is male biased. Polyandrous females reared 39% more offspring than socially monogamous pairs, and invested less parental care at each nest compared to monogamous pairs. Also, males that mated with polyandrous females compensated fully for the decrease in parental effort by females (Wiktander et al., 2000). This example strongly suggests that we must look at how social and ecological variables, as well as sexual selection, can influence male and female reproductive decisions.

2.2.2 Sexual conflict over mating

Since male and female interests are thought to be in conflict at the gametic level, it is suggested that males and females are in general in conflict with one another due to their differential investment in gametes and offspring (e.g. see Trivers, 1972; Houston et al., 2005, for conflict between the sexes over parental care), in which either the female or males wins, depending on which sex is best able to manipulate the other sex. Unlike sexual selection, sexual conflict theory argues that the coevolution of the sexes is driven by female resistance rather than female preferences (Chapman et al., 2003). Therefore, it is predicted that conflict over mating can result in accelerated antagonistic

coevolution, in which male behaviours and display traits become exaggerated as a response to female resistance.

Although the theory of sexual conflict has generated new and useful directions in evolutionary biology, some unaddressed issues remain: What are the costs and benefits of sexual conflicts? If sexual conflicts are costly, then how did the sexes evolve? Unfortunately, complementary aspects of sexual differences have gone largely unexplored, except for recent evidence suggesting that female mice seek out genetically compatible males as well as 'good genes' (Roberts and Gosling, 2003). Furthermore, recent studies have demonstrated that potential genetic benefits of mate choice are highly context-dependent, and thus challenge the idea that mating preferences are determined by static traits (Qvarnström, 2001). For example, in the Wax moth (*Achroia grisella*), the strength of the sexually selected trait, ultrasonic signalling, varied with the different rearing environments. Interestingly, the genotype that thrived in the most favourable environment failed to be successful in poor conditions (Jia et al., 2000). Therefore, favouring the most extreme traits does not mean that they will confer benefits in a wide range of environments and conditions, which may in turn favour plastic mate preferences as opposed to static ones (Qvarnström, 2001).

In conclusion, even the novel paradigm of sexual conflict, is largely influenced by Bateman's interpretations of sexual selection in *Drosophila*, leading to the interpretation that males will always attempt to re-mate, while females will "resist" many of these unwanted mating attempts (Wayne, 2000). However, this assertion is contradicted by experimental observations in three different *Drosophila* species, in which females approached males as often (or even more often) as males approached females. Also, some males were as discriminating (or even more so) than females (Gowaty et al., 2003). Female resistance describes how a female responds to having sperm from multiple males in her reproductive tract. Therefore, females often have control over determining the fathers of their offspring (Wayne, 2000). The drawback of sexual conflict models is that they centralise the importance of male reproductive behaviours, while females are often described as responding to males, rather than acting (at least to some extent) independently (Wayne, 2000). Thus, Wayne suggested that instead of

developing response models of females to sperm, researchers should investigate female behavioural physiology directly.

2.3 Alternatives to the "coy-female" hypothesis

Without denying that male-male competition and female choice do apply to many animal groups, there has been an ongoing persistence in evolutionary biology and animal behaviour to apply this model of sexual selection to groups it does not accurately represent. Also, there may be a bias toward the study of those animal systems that best represent the most acceptable gender stereotypes. Just four years after the publication of *Descent of Man and Selection in Relation to Sex* (Darwin, 1871), Antoinette Brown responded to Darwin's interpretations of sexual selection (see Fausto-Sterling et al., 1997). She argued that Darwin concentrated mainly on the selective pressures acting on males, which implied the evolution of male superiority and that females acquire some of these selected traits only by default. However, she suggested an alternative view, in which males and females of more complex organisms, evolve complementary characters. Unfortunately, during the Victorian era, females lacked the tools to back up their ideas with scientific evidence. However, the dominant sexual stereotypes reinforced by Darwin and his followers were finally overturned by the ongoing persistence of feminism in science.

It was previously assumed that male dominance was the norm in the structuring of primate societies (such as African baboons) while females passively accept the most dominant males (Fausto-Sterling et al., 1997). However, female scientists in particular, began to question the universality of such androcentric preconceptions of nature, playing a critical role in the re-evaluation of female and gender roles in general (Hrdy, 1986; Gowaty, 2003; Tang-Martinez and Brandt Ryder, 2005). The coy female hypothesis was first challenged in birds when it was observed that females visit other male territories in order to mate. However, perhaps the most critical of challenges materialised in the study of our closest relatives, the primates. Female scientists, with a keen interest in female behaviour and their relationships, collected vast amounts of 'unusual' data in females that went completely unnoticed by their male predecessors. Previous studies, which were largely male-biased, thus probably exaggerated the

amount of time spent observing males, whilst explaining away female behaviour with already established a priori assumptions (Fausto-Sterling et al., 1997).

For example, having studied primates for several years and several generations in the wild, Hrdy (1986) was able to determine which individuals mated with whom, which individuals approached the opposite sex, and finally the consequences of female sexual choices. Astonishingly for that time, the established orthodoxy that females are sexually uninterested and only discriminate keenly for the sake of fertilising their eggs was not supported by Hrdy's long-term studies in primates (Fausto-Sterling et al., 1997). For example, she demonstrated that in certain primate groups there is also competition between females over mating opportunities. Furthermore, many primates and female cats actively seek out males even when they are not ovulating or are pregnant at the time when they were soliciting males. For example, Meredith Small observed female Barbary macaques actively pushing males for sex (see Fausto-Sterling et al., 1997).

Counter to the idea that males are the primary organisers and controllers of the group, Strum (1987) provided evidence for the existence of female-based kin groups, which had a huge influence on the social lives of baboons. Since acknowledging the limitations of the male-male competition and female choice model, many new theories have been put forward to explain how females benefit from mating with different males (Hrdy, 1986). For example, the "manipulation hypothesis" derived from the increasing awareness that females in many animal groups (maybe not so much in those animals that don't rely heavily on good parenting) could do a lot to affect the survival of their offspring. Therefore, as well as their genetic contribution, males were also seen as crucial for offspring survival, in which good female politics could create essential male nurturers or at least encourage males to contribute other than providing their genes (Hrdy, 1986). Paternal care is common in many bird species. For example, in female rock sparrows (*Petronia petronia*), in which some females desert their first brood, the primary male mate takes over parental responsibilities and successfully rears young. Furthermore, the fledging success of the second clutches was significantly higher when females mated with previously unmated territorial males that defend nests, compared to when they mated with polygynous males (Pilastro et al., 2001). Although most theoretical models predict that males should first desert when there is a perceived risk of females deserting, this is not the case in rock sparrows, possibly because male parental

care is a sexually selected trait in this species (Griggio et al., 2005). The alpine accentor (*Prunella collaris*) is another example of how females can secure paternal care. In a study, it was shown that a female could secure paternal care if mated males received a threshold number of matings from the female, which increased his chances of paternity (Hartley et al., 1995).

2.4 Beyond the Primates

Primates have been of paramount importance for challenging androcentric biases in biology. However, the inadequacy of the Bateman paradigm was extended even further by a feminist scientist working in the same field of evolutionary genetics in *Drosophila*. Marta Wayne (2000) proposed a very different explanation of sex roles in these fruit flies, and critiqued the trend in *Drosophila* biology, which dichotomises the sexes. Wayne (2000) expressed particular concern towards the way sexual stereotypes often become naturalised and extrapolated to other animals including humans. However, the strength of Wayne's critique stems from her detailed knowledge of *Drosophila* behaviour, which does not conform in any way to Bateman's conclusions on male and female sex roles in these insects. Many scientists cite Bateman's paper wrongly, by claiming that female *Drosophila* mate only once or twice and purely for the sake of fertilisation. However, following her careful review of the paper, Wayne (2000) demonstrated that Bateman's data do not support the claim that females are coy, since they mate far more often than is necessary to ensure the lifetime fertilisation of their eggs.

Therefore, Wayne encouraged researchers to address the problem of the enduring commitment to the Bateman paradigm, and to propose credible scientific alternatives. The importance of these alternatives in science cannot be understated: Evolutionary psychologists were applying Bateman's rule to explain human rape, sexual harassment and jealousy by males (but not females) in the male quest to fertilise as many eggs as possible (see Wayne, 2000). Such cultural 'norms' are anything but appealing to females, nevertheless, these statements can be found in a multitude of publications (e.g. Pinker, 1997)

3. Competition and cooperation: from competing individuals to competitive and cooperative societies

3.1 Cooperation in the context of competition

One of the main assumptions in animal behaviour, which has profoundly influenced our understanding of animal relationships, is that competition between individuals or species is a primary condition. As a consequence of this logic, social relationships that involve altruistic behaviours will always reflect a degree of coercion or compromise (see Krebs and Davies, 1997). So far I have explored natural and sexual selection in relation to *competition* between individuals over sexual or non-sexual resources. These interactions are often easier to model compared with animals that live in large and complex social groups, since the latter often exhibit complex relationships of competition *and* cooperation (see reviews on the evolution of sociality: Alexander, 1974; Trivers, 1985; Bergstrom, 2002).

Many hypotheses have been put forward to explain the evolution of cooperation including kin selection (Hamilton, 1964; Riolo et al., 2001; Axelrod et al., 2004), reciprocity (Trivers, 1971; Bowles and Gintis, 2004) and multi-level selection (Wilson, 1997; Field, 2006). The latter theory of multi-level selection differs somewhat from the conventional view of natural selection, since it assumes that selection can operate on many different scales of biological organisation simultaneously. However, the prevailing view is that genes and the organisms that carry them are the ultimate 'units of selection' (Field, 2006). In this scenario organism behaviour should function to replicate genes (Dawkins, 1976). Based on this assumption, kin selection argues that cooperation between kin is favoured by selection, since kin share the same genes and therefore the inclusive fitness of an individual can be enhanced by preferentially cooperating with relatives. Social insects provide a strong case in support of the kin selection hypothesis, since as little as one individual can monopolise reproduction in the colony (see Queller and Strassmann, 1998).

However, altruistic behaviours are also common between non-genetically related individuals. Reciprocal altruism was proposed by Trivers (1971) to explain altruistic behaviours between kin and non-kin. Here, the idea is based on economic principles, so

that an individual aids another individual if the cost to the donor is less than the benefit to the receiver, and if the receiver is likely to reciprocate the altruistic gesture (Nowak and Sigmund, 1998). However, indirect reciprocity is also common in many human communities, in which altruistic gestures are not limited to dyads of interacting individuals (Trivers, 1971; Nowak and Sigmund, 1998). Therefore, the study of indirect reciprocity requires much more sophisticated models than the prisoner's dilemma, which is often used to study direct reciprocity (see Nowak and Sigmund, 1998). However, these models rely on the assumption that interactions can be indefinitely repeated and that these interactions can be maintained in large populations (Field, 2006), in which the payoff structure is far more difficult to assess. Reciprocal altruism in the form of tit-for-tat assumes that a player initially opts to cooperate but only continues to cooperate if the other player also cooperates. Tit-for-tat cooperation is likely to arise in two-person interactions if future encounters are likely. However, tit-for-tat in a repeated n-person prisoners' dilemma would predict cooperation only if all the participants cooperated previously. This poses a problem for explaining the stability of the cooperative strategy, even in relatively small groups, since just a few selfish players can undermine the benefits of conditional cooperators (Fehr and Fischbacher, 2003).

It is not surprising that cooperation and in particular altruism poses a problem for researchers in animal behaviour. For example, in female vervet monkeys (*Cercopithecus aethiops*) cooperation does not endow all individuals with equal fitness benefits: dominance rank was significantly correlated with birth rate when the distribution of food was clumped, which altered rank-related differences in diet (Whitten, 1983). Therefore, conflicts of interest may arise between group members for access to resources (Koenig, 2002). Other possible conflicts are between parents regarding how much each parent should invest into rearing their young (Trivers, 1972; Lazarus, 1990; Parker et al., 2002; Houston et al. 2005), or between parents and offspring (Trivers 1974; Parker et al., 2002). Despite such conflict, individuals living in social groups or engaging in some kind of social relationship have evolved a variety of behaviours aimed at resolving conflicts and maintaining cooperative relationships (Aureli and de Waal, 2000)

If this can be achieved then the benefits of social relationships and cooperative societies can be striking. For example, female Bechstein's bats (*Myotis bechsteinii*) recruit naive colony members to new roosts, a vital resource for the colony (Kerth and Reckardt, 2003). Some animals even refrain from reproduction and help others breed instead. For example, many birds are cooperative breeders, in which individuals help the breeding pair to rear their offspring rather than dispersing from their home nest to gain access to mates (for review see: Stacey and Koenig, 1990). Therefore, cooperation often requires certain individuals to pay more fitness costs compared to others. Despite these costs group living can benefit individuals, for instance, by making them less vulnerable to predation (e.g. The Alaskan moose, Molvar and Bowyer, 1994; the White-nosed coatis, Hass and Valenzuela, 2002; and the colonial Web-building spider, Uetz et al., 2002) and can enhance foraging efficiency (e.g. spotted hyenas, see Chapters 6 and 7).

3.2 Game theoretical models and the comprehension of social behaviour

Studies on social behaviour often apply the logic of game theory (Maynard Smith, 1982) to create models that predict the outcomes of evolution by natural selection when reproductive success depends on what other members of the population are doing (Hammerstein 1996; Weissing 1996). Game theoretical models were applied to the problem of mate desertion in social behaviour (Maynard Smith, 1977), e.g. males and females can choose between alternative courses of action called strategies, on whether to guard a batch of young or desert them. The costs and benefits of each strategy are defined depending on the course of action each individual adopts, which are then used to predict the circumstances that will favour a particular strategy over another. In the case of two individuals competing over a resource during a single encounter, game theoretical models predict that contestants will be more willing to fight if the costs of injury are low relative to the value of the resource (Krebs and Davies, 1997). However, if fighting is very costly then differences between the individuals, such as size or strength signify the outcome without aggression. Differences based on attributes such as size or fighting ability are called resource-holding potential (Parker, 1974; Hammerstein, 1981; Maynard Smith, 1982). However, other attributes that are not related to individuals' RHP can also influence the outcome of interactions such as the social ranks of individuals and their relatives (e.g. female spotted hyenas: Frank, 1986b).

Game theory models have been applied to a variety of studies on cooperation in humans and other animals. By predicting an individual's behaviour in different environmental and social contexts, it has succeeded in stimulating new insights into the evolution of sociality and cooperation. In his original formulation of the model, Maynard-Smith (1982) coined three essential components (taken from Houston and McNamara (2005):

1. **Strategies.** The set of strategies specifies the possible phenotypes, i.e. different ways in which an individual can behave.

2. **Payoffs.** The payoffs are the expected change in fitness associated with an action. The payoff depends not just on the action of the focal individual, but also on the actions of other members of the population.

3. **Stability criterion.** Game theory is an attempt to characterise the endpoints of evolution by natural selection. This requires a criterion to determine if an endpoint is stable.

One problem that can affect the consistency of game theory approaches is the assumption that there is a simple payoff structure, and that individuals can choose only between a small set of pre-determined strategies (Burtsev and Turchin 2006). For example, mate desertion decisions depend on what each parent does, and cannot be predicted by comparing the costs and benefits of desertion at a single point in time. This is because costs and benefits for both parents vary over the period of parental care, which influences their decisions to stay or desert (Lazarus, 1990). However, if interactions are considered independently from other interactions, then the resulting arbitrary payoff structure may not be consistent with the payoffs in other aspects of the system that were not included in the model (Houston and McNamara, 2005). Also, when the focal interaction is included in a wider context, and the assumption of fixed payoffs removed, then changes in reproductive success may be linked to changes in other components of the system, which influence and are influenced by the focal game.

Houston and McNamara (2005) concluded that game theoretical models should ideally include different aspects of the system, the future behaviour of players and the

behaviour of other population members in these different contexts of the whole system. They showed that many of the previous predictions in studies on parental care strategies could be altered when the focal game is included in a wider context. For example, when a model constructed by Maynard Smith (1977) to predict the probability of re-mating was modified to include the mating behaviour of other members of the population, Webb et al. (1999) found a mixed Evolutionarily Stable Strategy (when more than one strategy is maintained in a population by frequency-dependent selection; see Maynard Smith, 1982), rather than a pure Evolutionarily Stable Strategy (a single strategy that cannot be invaded by other strategies; see Maynard Smith, 1982), which was predicted by the model of Maynard Smith (1977).

Finally, in the context of evolutionary change and innovation, it is not always suitable to predetermine a set of defined strategies, since this limits our focus to those behaviours that are already known, while ignoring novel behaviours or strategies. Also, in this wider context it needs to be taken into account that the outcome of the game both influences and is influenced by the payoff structure (Houston and McNamara, 2005).

4. Conclusion

In conclusion, I have provided a broad and critical overview of the various types of competition in animals and the hypotheses used to explain the evolutionary outcomes of competition both between and within the sexes. Many traditional approaches to the study of sexual selection have tended to prematurely stereotype the sexes in the absence of convincing evidence. However, feminist perspectives have challenged what has become known as the Darwin-Bateman paradigm (Dewsbury, 2005) by providing evidence that demonstrates the alternative to the coy female hypothesis. I also discussed challenges to the conventional logic of competition, such as the lek paradox and the evolution of cooperative relationships. I propose that a more realistic understanding of the nature of competition and animal relationships requires that we address these paradoxes. Also, to understand how competition may generate diversity, we need to acknowledge the link between competition and innovation. Therefore, rather than simply assigning limited resources to the best-adapted individuals, competition may drive animals to discover novel opportunities, which may result in adaptive solutions. I return to this topic later on in my discussion and interpretations of my findings.

Chapter 2: *Aims, objectives, and rationale*

Gina Raihani

1. Main research problems

My critical overview and critique of the conventional logic of competition addressed two main issues. First, I explored the logic of competition and the challenges that it poses for our understanding of fitness gradients and how they are maintained in populations. A classic example is the paradox of the lek (Borgia, 1979), which predicts the depletion of genetic variation, since it is supposed that females should always select the highest quality males. However, in reality the opposite occurs: diversity is generated and maintained in populations of lekking animals. I also discussed the logic of competition in the context of cooperation, which poses a challenge for the neo-Darwinian paradigm, especially when trying to explain the origins of altruism and reciprocity.

My other research problem addresses gender issues, which follows from my critique of conventional models of competition, but more specifically on competition over mating opportunities. I challenged the generality of the Darwin-Bateman (Dewsbury, 2005) paradigm and discussed the alternatives proposed by feminist biologists. These feminist critiques expose many of the problems associated with androcentric conceptualisations of the sexes, which tends to stereotype females as choosy but sexually coy, and males as sexually assertive and indiscriminate. Although the Darwin-Bateman paradigm does indeed apply to certain situations, many studies (especially in primates) have demonstrated that male and female sexual behaviours cannot be predicted on the basis of pre-assumed sexual stereotypes, but rather on their life-history, ecological and social circumstances (Gowaty and Hubbell, 2005).

1.2 Larger research objectives

In this thesis, my specific research questions are nested within a larger research domain of enquiry. First, one of my main aims is to investigate diverse contexts of competition in animals. I initially chose to investigate competition because of the huge phenotypic diversity it can generate. For example, intraspecific competition appears to influence disruptive selection towards large or small gill rakers in the three-spine stickleback (*Gasterosteus aculeatus*), which show substantial within-population niche variation (Bolnick, 2004). Therefore, it is necessary to understand the exact mechanisms that

generate and maintain individual variation, since differences between individuals, that are beneficial in different contexts, can lead to diverse selective pressures acting on them, as observed in the sticklebacks. However, as discussed in the previous Chapter, the conventional logic of competition can also pose a challenge for explaining how such diversity is created and maintained (see Chapter 1: The lek paradox and the paradox of plankton; also see section 3.3, Chapter 7). Sexual selection in particular can generate striking differences between and within the sexes, and between species (Andersson, 1994). Thus, competition over reproduction offers a huge variety of interesting research opportunities for exploring both micro-and macro-evolutionary patterns and trends.

The way we investigate competition in males and females is often influenced by prescribed gender-biased assumptions. For example, spotted hyenas, in which females are the dominant sex, have been labelled as hyperaggressive without convincing evidence (see review: East and Hofer, 2002) Therefore, I also address the problem of gender stereotypes, and the way in which they have misrepresented a number of animal systems. Here, my aim is to explore the extent to which such stereotypes apply to the animal kingdom, using spotted hyenas as an example, and the resulting stigma that can result when the sexes do not fit into prescribed gender categories.

Finally, another aspect of animal behaviour, which attracted me to the subject of competition, is the challenge that the conventional logic of competition poses for the understanding of how fitness gradients are maintained in populations. Therefore, my third research question concerns itself with the active role of behaviour and flexibility for generating novel evolutionary opportunities (Bateson, 2004). In this scenario the assumption is that behaviour both influences and is influenced by diverse contexts and intensities of competition.

1.3 How I address these Research Questions

I address my larger research questions using two different but complementary approaches. First, I investigate direct and indirect competition over reproduction in bustards, American rubyspot damselflies and spotted hyenas. Reproductive competition is broader than mating competition, because it includes competition over resources that can enhance individual reproductive success. These studies fit into my overall research

questions, because they each address different aspects of competition (I review these in my next Chapter), which generate differences both between and within species. Therefore, this approach allowed me to investigate the diverse evolutionary patterns, and consequences of competition in different animals. Also, in spotted hyenas I explore the problem of gender-biased assumptions by discussing the ways in which these assumptions have misrepresented these animals both in science and culture. I believe this is important because, not only does the questioning of conventional gender categories make us aware of the misrepresentation of the sexes, but it may also benefit other domains of enquiry, which are not directly related to gender.

1.3.1 The influence of sexual selection and male agility on sexual size dimorphism (SSD) in bustards (Otididae)

In bustards I investigated patterns of sexual size dimorphism (SSD), differences in sizes between the sexes, and how they are influenced by different intensities and types of competition. SSD is ideal for investigating the effect that sexual competition can have on morphological characters, since diverse forms of sexual competition can result in different degrees and directions of SSD (Székely et al., 2007). This was an excellent opportunity to pursue my interest in competition and social behaviour, since sexual selection in particular gives rise to a huge diversity in social behaviour and phenotype.

Bustards are ideal for studying sexual size dimorphism, since they exhibit a huge variation in patterns of SSD, ranging from male-biased to female-biased SSD, including monomorphic species. Using this interspecific variation I tested functional hypotheses of SSD using phylogenetic comparative methods (see Chapter 4). This was a cross-species comparative study for which I collected published and unpublished data on 25 species of bustards. I investigated intra- and inter-sexual selection and their influences on male mating behaviour and patterns of sexual size dimorphism (I review SSD and the hypotheses proposed to explain the evolution of SSD in my next Chapter). Sexual selection predicts large male size in relation to female size in polygynous species, and a less or no sexual size dimorphism in more monogamous species. Sexual selection also predicts that in species in which males display or compete on the ground, males should be larger than females, whereas males should be smaller relative to females in species where males compete or display in the air.

1.3.2 Male mating tactics in the American Rubyspot damselfly

Mating competition can result in differences between individuals of the same species as well as differences between species, which is what I investigated in bustards. While cross-species analyses are useful for investigating macro-evolutionary trends and patterns, it should ideally be complemented with field studies and experiments, which focus more specifically on the underlying processes of competition. To explore these processes, I chose to investigate alternative reproductive behaviours (ARBs) in odonates. ARBs are ideal for investigating the relationship between plasticity in behaviour and competition, because ARBs are often condition-dependent in odonates.

Odonates are ideal for investigating ARBs, because they exhibit a huge variety of territorial and non-territorial mating tactics and are easy to identify and manipulate in the field. Also, generation times are shorter in odonates compared to birds or mammals, which makes it possible to identify changes in mating behaviour that occur over an individual's life span. In my study on the American rubyspot damselfly, I investigated male competition over reproduction by exploring their ARBs in the field. Here, my main objective was to investigate alternative mating tactics in this species and to explore whether males can adjust their mating behaviour in a way that matches their competitive ability. In this species mating success is greatly enhanced by their ability to defend territories along streams and rivers, which in turn depends on the amount of fat thoracic reserves available. This is because territory defence requires huge energetic demands, depending on the intensity of male-male competition over these reproductive sites. Also, fat reserves in adults cannot be restored, so once males lose their fat reserves, the chances for obtaining new territories are significantly lower.

Previous studies have distinguished between territorial and non-territorial males, in which the former obtains significantly more matings compared to the latter. However, I discovered a third reproductive tactic: switching, in which males exhibit both territorial and non-territorial tactics. Given these three tactics, I tested whether any differences could be observed in their mating success, amount of fat reserves, and survival.

1.3.3 Competition, cooperation and the dynamic structuring of social formations in Spotted Hyenas

This study on spotted hyenas differs somewhat from my studies on bustards and American rubyspot damselflies, because animals that live in social groups need to behave in a manner that maintains cooperative relationships while also fulfilling individual food and reproductive requirements. Also, while my other studies focused mainly on male mating behaviour, in spotted hyenas I specialised mainly on females and their competitive and cooperative interactions. In this Chapter I first address the problem of fixed gender categories and how these have led to the stereotyping and misrepresentation of the spotted hyena in culture and science. Spotted-hyenas are ideal for investigating issues surrounding gender, because they exhibit behaviours and morphologies, which do not fit into our 'normal' gender categories. This is emphasised most strongly by the fact that females are the dominant sex and almost indistinguishable from males. These animals have been labelled as antisocial in culture, and hyperaggressive in science. However, long-term studies in the Serengeti have contradicted this view of spotted hyenas. Therefore, to explore the 'true nature' of these widely misunderstood animals, I review the literature and my own observations in the field to see whether these claims are supported by strong scientific evidence.

I adopted two different methods for my behavioural observations of spotted hyenas in the field. First, I recorded any type of behaviour or behavioural interactions, which I found either interesting or unusual. I interpreted these observations from my own perspective, which was however complemented by published and unpublished data from an expert on spotted hyenas. Therefore, in the discussion of my observations, I include my own interpretations as well as discussions with Marion East.

Since my thesis researches different types of competition in animals, I also focused more specifically on female coalitions in spotted hyenas. I investigated female coalitions, rather than other types of competition because they occur on a daily basis at the communal den, where females nurture their cubs and engage in social interactions. Therefore, I was able to collect enough data for my 5-week fieldwork period. Also, coalitions are consistent with my studies on bustards and American rubyspot damselflies, since they are a form of reproductive competition. This is because

coalitions are important for the maintenance and acquisition of social rank, which determines access to resources in the clan territory, and thus increases reproductive success due to enhanced offspring survival.

A coalition typically includes an initiator, target, and one or more supporters. Thus, to investigate the pattern and process of competitive relationships in female spotted hyenas, I recorded which individuals initiated coalitions, which were targeted, and the supporters of coalition initiators. Using this data I was able to explore the relationships between the social ranks of different coalition members. First, I investigated the relationship between the social rank of initiators and their targets. Then, I tested whether there was a significant correlation between initiators and their supporters, and finally I explored the relationship between all coalition members (initiators plus supporters) and the targets of the coalition.

Since spotted hyenas live in a matrilineal social system, similar to many cercopithecine primates, I predicted that associations in female spotted hyenas follow a pattern similar to those predicted by Seyfarth's (1977) model of primate affiliative behaviour. This model predicts that low-ranking females are attracted to high-ranking females, leading to competition between females over access to high-ranking females. This results in females tending to associate with those next to them in the hierarchy, since competition prevents low-ranking females from accessing top-ranking animals. Therefore, I expected female spotted hyenas to associate mainly with adjacent animals in the hierarchy. Also, since coalitions entail a high risk of injury, due to the possibility of aggressive conflicts, I also predicted that high-ranking females engage more frequently in coalitions, compared to low-ranking females, because high-ranking females have priority access to resources in the clan territory and hence higher reproductive success, compared to lower-ranking females. Therefore, a similar drop in rank for a dominant animal and a lower-ranking female may be more costly for the high-ranking female if she suffers a higher reduction in feeding rights in the clan territory, compared to the lower-ranking female. Thus, it is predicted that high-ranking females will try to maintain their 'privileged' position in the hierarchy when the benefits of securing social rank outweigh the potential cost of injury.

1.4 Summary of my findings

My study on bustards supported the predictions of sexual selection, since both mating system and male display agility were significant predictors of SSD when controlling for each other's influence. Also, our results were consistent with Rensch's rule (an allometric relationship between SSD and body size), which showed that bustards exhibit one of the strongest allometric relationships in any avian taxa. The evidence suggests that body size (a morphological trait thought to be under strong phylogenetic constraints) responds to increasing levels of competition.

Second, when I investigated the plasticity of male territorial behaviour in the American rubyspot damselfly (*Hetaerina americana*), I found, contrary to what has been documented in previous works, that males exhibit an alternative reproductive strategy to the "fixed" territorial and non-territorial tactics. This is the first study to identify an alternative reproductive strategy in this species: switching, in which males switch from territorial behaviour to non-territorial behaviour and vice versa. Interestingly switcher males had an intermediary amount of fat reserves, while territorial males had the most and non-territorial males had the least fat content. This strongly suggests that male mating tactics are influenced by their energetic status. When comparing territorial, non-territorial and "switcher" males, I found that mating success did not differ between the three tactics, and that switcher males survived longer than territorial and non-territorial males. My findings are novel, since it was previously thought that males only switch once from territoriality to non-territoriality during their life span, due to energetic reasons.

Finally, I extended my investigation of competition between males, to include female competition in spotted hyenas. First, spotted hyenas do not represent the hyperaggressive image with which they are frequently associated. Also, contrary to many of the cultural depictions of spotted hyenas, in which they are portrayed as stupid, cowardly and greedy, I demonstrated that these are nearly all based on false underlying assumptions regarding gender 'norms'. In my study on female coalitions, my results revealed that the social ranks of coalition partners and their targets were correlated, and higher-ranking females were more likely to form coalitions compared to low-ranking individuals. This confirms the prediction that coalitions between adjacent individuals in

female spotted hyenas (similar to many cercopithecine primates) result in the stability of the dominance hierarchy, thereby maintaining the status quo.

2. What do these studies say about the role of behaviour in evolution?

Finally, I address my final research question by integrating my three diverse studies into a coherent framework, which looks at the way these animals respond to changes both in their local (e.g. condition, size, age etc...) and non-local (ecological, social, etc...) circumstances. While mating behaviour in bustards appears to be largely dependent on body size, in odonates, ARBs are influenced by individual condition. Finally in spotted hyenas, the pattern of coalition formations reveals that competition in the female dominance hierarchy is most salient amongst higher-ranking females, and associations between females are not random but dependent on social rank.

To complement my own findings in these animals, I review more evidence, suggesting that these animals attune their behaviour in a way that suits their individual, social and ecological circumstances. First, I address this question in bustards by reviewing the literature on the plasticity of mating systems in response to variations in ecological circumstances. Then, I reviewed ARBs in odonates, which appear to be influenced not only by male condition but also by female tactics and their mating behaviours. Finally, I also review evidence for behavioural plasticity in spotted hyenas, by comparing the different foraging tactics of these animals living in different eco-systems throughout Africa.

My final research objective addresses the question of how such behavioural plasticity can be explained in an evolutionary framework. In this section I challenge the conventional view of competition, because it is based on the assumption that novel adaptations are necessarily preceded by changes in the genes. However, if this were strictly the case then one would expect high-quality individuals to systematically replace low-quality individuals in a population, unless a proportion of the population becomes genetically adapted to a pre-existing ecological niche, or are able to exploit different resources. However, these explanations are not complete, because adaptation alone does not explain how animals discover and in fact construct novel opportunities (see Baldwin, 1896).

Therefore, I discuss the alternatives to the conventional logic of competition by invoking the importance of behavioural flexibility for generating novel evolutionary opportunities. The idea that learned behaviours can influence the direction and rate of evolutionary change by natural selection, was initially developed by James Mark Baldwin in 1896 (see Dephew, 2003). I propose that these arguments, featuring in theories such as phenotypic plasticity (see West-Eberhard, 2003), can benefit our understanding of how fitness gradients are **generated** and maintained in populations. Phenotypic plasticity argues that the behaviours that animals adopt may have consequences for their subsequent evolution, suggesting that behaviour can in fact influence the direction of evolution, rather than simply being 'driven' by selection. Phenotypic plasticity may explain 1) why organisms with near identical genotypes can express alternative phenotypes, 2) how animals can modify their behaviour depending on their circumstances and 3) why animals previously adapted to a particular environment can survive when suddenly subjected to novel conditions. I propose that these issues raised by phenotypic plasticity are essential for the integration of my studies into a coherent framework, because it allows me to explore the connections between my studies, namely the way in which animals respond to and influence diverse contexts of competition.

Chapter 3: *Background review*

1. The evolution of sexual size dimorphism

2. The evolution of alternative reproductive behaviours

3. Competition, cooperation and the evolution of female coalitions in matrilineal social formations

Gina Raihani

A key to understanding evolutionary change is to understand how animals uniquely respond to competitive situations. Therefore, in each of my specific study groups I explored competitive processes and tested alternative hypotheses regarding the outcomes of both direct and indirect competition over reproduction.

In my last Chapter, I explained why I am interested in competition, and how my studies are suitable for my research aims and objectives. In this Chapter I review the topics explored in my study groups. First, in bustards I explored the relationship between male morphology and behaviour, and inter and intra- sexual selection, while in American rubyspot damselflies, I investigated how males of different competitive ability manage to obtain mating opportunities via the adoption of alternative mating tactics. In spotted hyenas, reproductive success is largely influenced by the position a female holds in the female dominance hierarchy, and females try to maintain their social rank by forming coalitions or alliances. Therefore, I investigated the patterning of coalition formations in female spotted hyenas, and discuss their potential functions and significance for competitive and cooperative relationships in the female dominance hierarchy.

I begin this Chapter by reviewing the field of sexual size dimorphism -- the differences in size between the sexes -- and the hypotheses used to explain its evolution. Then, I explore the evolution of alternative reproductive behaviours exhibited by males, but also (and importantly) by females. Finally, I review the nature of relationships of dominance and submission, with a special focus on matrilineal dominance hierarchies in which coalitions often, but not always, play a critical role in the structuring of female relationships.

1. The evolution of Sexual Size Dimorphism

"The degree of sexual dimorphism in size...is the result of the difference between the sum of all the selective pressures affecting the size of the female and the sum of all those affecting the size of the male." (Ralls, 1976, p. 259)

Males and females are rarely the same size. Such difference in size across species is termed sexual size dimorphism (SSD). For example, in territorial cichlid fish *Lamprologus callipterus*, males can be up to 12 times heavier than females (male-biased SSD; Schütz and Taborsky, 2000), whereas in the Blanket Octopus (*Tremoctopus violaceus*), females can be up to 40,000 times heavier than males (female-biased SSD; Norman et al., 2002). Females are larger than males in most invertebrates, amphibians and reptiles, while males are usually the larger sex in birds and mammals (Andersson, 1994; Fairbairn, 1997; but see Ralls (1976) for mammals in which females are the larger sex).

Darwin (1871) suggested that fecundity selection in females and sexual selection in males favours the evolution of larger body size in many organisms. Ever since Darwin first drew attention to the evolution of SSD, many hypotheses have been proposed to explain how SSD evolves (reviewed by Jehl and Murray, 1986; Hedrick and Temeles, 1989; Andersson, 1994; Blanckenhorn, 2005; Fairbairn et al., 2007). Although Darwin's original ideas have remained central to the understanding and study of SSD, their explanatory power has remained controversial (Blanckenhorn 2005). Here, I will first describe the various hypotheses that have been proposed to explain the evolution of SSD.

1.1 Hypotheses

1.1.1 Sexual selection

First, sexual selection may favour large male body size in those contexts in which males engage in contests over females (intrasexual selection). For example, large males may have an advantage in contest competitions that determine access to mates (Clutton-Brock and Harvey, 1977; Mitani et al., 1996; Owens and Hartley, 1998; Dunn et al., 2001; Lindenfors et al., 2003). However, large size is not always advantageous, especially when the competition takes place in the air (Payne, 1984; Jehl and Murray, 1986; Figuerola, 1999; Székely et al., 2000; Székely et al., in prep). If agility and manoeuvrability confer an advantage to males competing in the air, then sexual selection should favour smaller males (Andersson and Norberg, 1981). This may be reinforced if females prefer to mate with smaller males (intersexual selection). This

pattern exists, for example, in shorebirds and seabirds, in which evolutionary increases in male agility are correlated with evolutionary changes toward female-biased SSD (Székely et al. 2000, 2004; Serrano-Meneses, and Székely, 2006). Thus, intersexual selection via female choice is also thought to influence the degree and direction of SSD.

1.1.2 Fecundity selection

Second, fecundity selection for increased female size has been proposed to explain why females are larger than males in most cold-blooded organisms (Andersson, 1994; Blanckenhorn, 2005). Darwin (1871) suggested that large size might be favoured in females, since larger females can sustain a larger number of eggs. For example, egg production increases in larger females, including the ability to store energy reserves (Andersson, 1994). Fecundity selection has been supported by studies in insects (e.g. Preziosi et al., 1996), and spiders (e.g. Prenter et al., 1999), which have shown positive relationships between body size and fecundity. However, there are also advantages of small size for females such as earlier and more rapid reproduction (see Table 1). Therefore, it is always important to incorporate life-history traits as well as the costs and benefits of large or small body size for a given species in studies on SSD.

1.1.3 Differential niche utilisation

Third, ecological factors may also influence the morphology of the sexes, resulting in SSD (Selander, 1966). This differential use of resources between the sexes can help reduce competition over food between males and females when resources are scarce. For example, in the purple-throated Carib Hummingbirds (*Eulampis jugularis*; Temeles *et al.*, 2000), males and females feed from different flowering plants, and each sex has evolved a distinct culmen that corresponds to the length and curvature of the specific flowering plant they use to feed from. Nevertheless, studies in other birds, such as shorebirds, gulls and alcids, do not provide support for the differential niche utilisation hypothesis, since despite the expectation that biparental species should exhibit more divergence in their feeding apparatus (i.e. bill length and shape) compared to uniparental species, the differential niche utilisation hypothesis did not explain the observed variation in dimorphism (Székely et al., 2000).

Table 1. Selective factors that may influence the sizes of sexes, and the direction and degree of sexual size dimorphism (taken from Andersson 1994).

Female advantages of large size: Higher fecundity; better parental care; male preferences for large females; dominance in contests over resources, or over males in role-reversed species.
Female advantages of small size: Earlier maturation, with shorter generation time and more rapid reproduction as conditions become favourable; more effective shunting of resources into offspring production
Male advantages of large size: Dominance in contests over females or resources when strength is crucial; better performance in endurance rivalry; female preferences for large males; higher success in sperm competition
Male advantages of small size: Dominance in contests over resources when manoeuvrability rather than strength is crucial; earlier maturation, with more rapid reproduction and shorter generation time; higher success in scrambles; more surplus energy available in searching for mates; female preferences for small males

1.2 Rensch's rule

Many animals exhibit an allometric relationship between the degree of SSD and body size, which results in a larger degree of SSD in species where males are the larger sex and a smaller degree of SSD in species where females are the larger sex (Fairbairn, 1997). This allometric trend has been termed Rensch's Rule (Rensch, 1950; Fairbairn, 1997) and it has been documented in a wide range of animal taxa, including mammals (Ford, 1994; Abouheif and Fairbairn, 1997), birds (Payne 1984; Björklund, 1990; Webster, 1992; Colwell, 2000; Raihani et al., 2006; Székely et al., in prep.), reptiles (Abouheif and Fairbairn, 1997) and insects (Sivinski and Dodson, 1992; Colwell, 2000).

Sexual selection is likely to contribute to allometric patterns of SSD (Abouheif and Fairbairn, 1997). In the only comparative test of sexual selection and its relationship with Rensch's rule to date, Székely et al. (2004) found that Rensch's rule exists in

shorebirds, which appears to be determined by male display type and the intensity of sexual selection.

Despite the advantage of agility for small males over larger males, the disadvantages of large body size are comparatively rare in the literature (Blanckenhorn, 2000). These include viability costs in juveniles due to long development and/or fast growth; increased risk of predation, parasitism or starvation; decreased mating success of large males due to reduced agility and/or high energy requirements; and finally decreased reproductive success in both sexes due to delayed reproduction (Blanckenhorn, 2000).

For example, in many insects, growth to a large body size is associated with a longer developmental time (Roff, 1992). Thus, significant fitness costs, due to delayed reproduction, are inevitable if males delay development for too long, (Rowe et al., 1994; Johansson and Rowe, 1999; Plaistow and Siva-Jothy, 1999).

1.3 Phenotypic plasticity and the evolution of SSD

In a study, Blanckenhorn (1998) showed that flexible growth rates in the yellow dung fly (*Scathaphaga stercoraria*) were facilitated by low genetic correlations between developmental time and body size, which enabled larvae to adapt their body size and growth rate to the abundance of food and the degree of competition with other individuals. Sexually selected traits are often predicted to be more plastic in their expression, in which individuals in high condition develop more elaborate characteristics (Price, 2006). It has been suggested that the widespread patterns of intraspecific variation in SSD in many insects support the differential-plasticity hypothesis, in which traits that contribute to reproductive fitness are "adaptively canalised" (Fairbairn, 2005).

In her study, Fairbairn (2005) tested the differential phenotypic plasticity hypothesis and the sexual selection hypothesis in Water striders (*Aquarius remigis*). Unlike the sexual selection hypothesis, which predicts that differences in body size are due to genetic adaptation to local patterns of selection, the differential plasticity hypothesis claims that changes in body size can be environmentally induced, and to a larger degree in the more plastic sex. In Water striders, in which the ratio of female to male size is less than 1.2, males often exhibit higher phenotypic plasticity in body size compared to females (see Fairbairn, 2005). To test both the sexual selection and phenotypic plasticity

hypothesis, Fairbairn (2005) subjected Water striders to environments with different temperatures. According to differential phenotypic plasticity, males should respond more strongly than females to the temperature regime. However, if body size is driven by sexual selection, one would expect males to show more variation in body size compared to females under each environment. The results of the study did not support the hypothesis that diversifying sexual selection drives allometry for SSD in water striders, but instead, patterns of allometry and phenotypic plasticity appeared to be influenced by greater phenotypic plasticity in males compared to females. Male and female reproductive traits were most likely to be canalized against the effects of temperature, suggesting that such sex-specific plasticity is adaptive (Fairbairn, 2005). The influence of phenotypic plasticity on sexual size dimorphism at the species level and in higher clades remains to be tested, and in particular the co-influence of sexual selection and phenotypic plasticity, which are unlikely to be mutually exclusive.

In conclusion, the evolution of SSD is likely to influence and be influenced by animal life histories, behaviour, development and ecology. The study of SSD and the processes that generate differences between the sexes provide an array of research opportunities that enhance our knowledge of evolutionary processes, in particular, the combined effect of natural and sexual selection on the differentiation between the sexes (reviewed by Blanckenhorn 2005; Fairbairn et al. 2007). Nevertheless, what has been referred to by Blanckenhorn (2005) as the 'ghost of SSD evolution past', is the main problem facing researchers, namely how to separate the causes of SSD from the consequences of SSD for present ecology and behaviour. Thus, the many hypotheses that have been used to explain the evolution of SSD should ideally be integrated in order to gain a comprehensive understanding of the processes underlying SSD.

Also, comparative phylogenetic approaches (patterns) should be combined with single-species studies (processes), since the cross-species comparative approach alone cannot identify the underlying behavioural mechanisms that generate the identified patterns. Therefore, "a combination of both approaches is the best way to link pattern to process, as one central paradigm of evolutionary, ecological and behavioural research is that macroevolutionary patterns result from micro-evolutionary processes" (Blanckenhorn, 2005, p. 1005).

2. The evolution of alternative reproductive behaviours

In the previous section, I described three hypotheses that have been proposed to explain the evolution of differences in body size between the sexes. Sexual selection in particular has gained much support for the rapid evolution of particular traits and behaviours. However, more recently researchers have generated a large body of evidence demonstrating that differences between individuals of the same sex are also widespread throughout the animal kingdom. In particular, much research has focused on the evolution of alternative reproductive behaviours (ARBs) (Austad, 1984; Dominey, 1984; Caro and Bateson, 1986; Gross, 1996; Taborsky, 2001). A number of studies have now demonstrated that evolution does not give rise to a single best male and female phenotype, but rather to a huge range of phenotypic diversity (Gross, 1996). ARBs have so far been used to explain the variety of phenotypes and behaviours that enhance reproductive possibilities.

2.1 Male reproductive strategies and tactics

The scarab beetle (*Onthophagus taurus*) provides a nice example of ARBs. In this species males are dimorphic: larger males develop long curved horns while males that don't reach a certain body size remain hornless (Moczek and Emlen, 2000). Horned males defend tunnel entrances (which contain females) by engaging in aggressive fights, while smaller males adopt a non-aggressive sneaking strategy to avoid competitively superior males. Although large size is clearly advantageous when engaging in fights, smaller size enhances manoeuvrability, which is advantageous when adopting a sneak strategy.

It has been considered that fish exhibit the largest diversity in male competitive and cooperative reproductive behaviours (Taborsky, 2001). Taborsky (2001) used the term "bourgeois tactic" to describe those males that seek to gain primary access to mates or fertilizable eggs, while males that attempt to evade the monopoly of "bourgeois" males are described as "parasitic". Courtship behaviour and resource defence are typical for bourgeois males, while sneaking or streaking behaviours are common in males when adopting the parasitic tactic (Taborsky, 2001). Two examples of the parasitic tactic include sneaking or female mimicry. In the former, males usually lack sexually selected

traits, such as body ornamentation, but with their stealth and speed they occasionally gain fertilisations by leaving sperm on the nests of bourgeois males during spawning. Alternatively, some males mimic females, in which they trick bourgeois males into gaining access to their spawning sites (Mank and Avise, 2006). Conversely, a cooperative association can also develop between resource holders and secondary males. For example, secondary males can gain mating opportunities by participating in mate attraction and defence (see Taborsky, 2001).

Alternative male mating tactics are also found in territorial odonates (Corbet, 1999). Nevertheless, only few species show marked morphological differences between the territorial strategy and the alternative mating strategy. In such cases, the morphological differences are so conspicuous that they are denominated morphs (Corbet, 1999). For example, territorial 'fighter' males of the damselfly (*Mnais costalis*) are orange-winged and significantly larger than the clear-winged, non-territorial 'sneak' males (Tsubaki et al., 1997). Although the orange-winged fighter males have a higher daily mating rate, overall reproductive success does not differ between the morphs, because the reproductive life span and longevity is significantly higher for clear-winged males compared to orange-winged males (Tsubaki et al. 1997). Plaistow and Tsubaki (2000) compared the associated developmental and reproductive costs for the two morphs. In orange-winged males, adult reproductive costs resulted in fat reserves decreasing with age, while this trend did not exist in clear-winged males, in which their fat content remained constant throughout their lives. Also, this study found that orange-winged males gained double the amount of body mass between emergence and reproduction, compared to clear-winged males, which strongly suggests that development is more costly in orange-winged fighter males.

Taken together, the findings of this study suggest that selection operates differently on body size in these male morphs, since large body size increases mating success in orange-winged males, whereas it appears to confer no advantage to clear-winged males. Odonates are ideal subjects for exploring speciation and diversification of traits, since insects have low generation times, making evolutionary processes easier to observe. In fact, in a few populations in which orange-winged males are absent, clear-winged males have been observed to exhibit a range of mating behaviours that include territorial, non-territorial and opportunistic tactics (Siva-Jothy and Tsubaki, 1989a, 1989b).

ARBs exist throughout the animal kingdom. In ruffs (*Philomachus pugnax*: Widemo, 1998) for example, the majority of males defend territories on leks, while other males behave as satellites and are allowed to access territories belonging to residents as long as they behave submissively. Widemo (1998) found that the presence of satellites in leks correlated with an increase in visits by females. He proposed that this pattern can be explained by the ability of satellites to track female movements, and that females are more attracted to coupled pairs (i.e. a combination of residents and satellites). Males exhibiting the different strategies thus benefit from one another, and the lifetime fitness benefits are equal for both the strategies. Therefore, it is suggested that the alternative mating strategies of the ruff are typical of a frequency-dependent mixed ESS (Maynard Smith, 1982), in which fitness pay-offs are equal for residents and satellites.

2.2 Female alternative reproductive strategies and tactics

Scientists have mainly focused on ARBs in males, however, in fish (a group in which ARBs have been studied extensively in males) relatively little attention has been directed towards ARBs in females, despite their very obvious existence (Henson-Alonzo and Warner, 1997). For example, in guppies, females can choose mates either independently, or by copying the mate choice of other females. This is thought to be adaptive if females differ in their ability to assess mates, or if the costs of mate choice are high. In fact, younger females are more influenced by the decisions of older females but not vice-versa, which suggests that younger females may be less experienced in assessing mates. However, this tactic also depends on whether the opportunity arises to observe the mate choices by other females (see Henson-Alonzo and Warner, 1997).

One reason for why female ARBs have been largely ignored may be due to the frequent assumption that ARBs evolve as a consequence of a "winner-takes-all" scenario, in which males with the highest competitive ability are able to monopolise reproduction. Therefore, 'inferior' males need to adopt alternative tactics, which does not require the direct competition with 'dominant' males. However, Henson-Alanzo and Warner (1997) pointed out that this "winner-take-all" situation is not the only, or even most common, scenario. Instead, they argue that studying the interactions between the sexes is crucial for understanding the evolution of ARBs in both sexes, since at least in the context of

mating, the behaviour of one sex is likely to influence the behaviour of the other sex. For example, despite the frequent observation of males fighting over territories, the territory that results in the highest mating success for one male will be determined by female mating decisions. Therefore, the existence of the alternative male mating tactics depends on whether females are willing to mate with either type. In turn, female choice will depend on variations in male and territory quality. Henson-Alonzo and Warner (1997) thus concluded that females play an important role in determining the mating success of males of different types, and the resulting skew in mating success may lead to the evolution of male ARBs, which in turn leads to variation in female choice and reproductive behaviour.

2.3 The evolution of alternative reproductive strategies and tactics

Evolutionary game theory can be used to explain the evolution of alternative reproductive tactics, which initially provided two possible explanations. First, it was proposed that alternative reproductive tactics could be maintained by a mixed evolutionary stable strategy (ESS), in which alternatives are maintained by frequency-dependent selection (Maynard Smith, 1982). Conversely, condition-dependent fitness may also contribute to the maintenance of alternative reproductive tactics, in which the fitness of a particular ARB depends on particular aspects of the individual or their environment (Gross, 1996). It is argued that condition-dependent alternative reproductive tactics should evolve if individuals compete over mates or resources and that success depends on age, experience, energy reserves or size. If the fitness-condition relationship differs between the alternative tactics, then these tactics should be maintained in the population.

One would expect that a conditional strategy, in which an individual adopts a strategy that best suits its state, should always be favoured by selection over a mixed ESS consisting of heritable pure strategies (Plaistow et al., 2004). However, although most game-theoretical models support this idea (e.g. Calopterygid damselflies, Forsyth and Montgomerie, 1987), there are also examples of mixed ESSs with genetically determined pure strategies, which are maintained by frequency-dependent selection (Plaistow et al., 2004). For example, the orchid *Dactylorhiza sambucina* maintains a flower-colour polymorphism of yellow and purple flowers in natural populations

throughout Europe. In a manipulative experiment Gigord et al. (2001) showed that negative frequency dependent selection maintains flower-colour polymorphism via pollinator preference for rare morphs. Finally, in a model designed by Plaistow et al. (2004), they show that mating skew probably plays the most important role in determining whether a population of individuals will adopt a pure or conditional strategy. First, when mating skew is extremely high (i.e. unevenly distributed), then competitive ability becomes an important factor, since only the best quality males can obtain territories. However, for a given cost and limit of plasticity, conditional strategies are more likely to become established in populations with intermediate levels of mating skew, since conditional individuals are unlikely to attain a level of competitive ability necessary for obtaining a territory and thus depend on females that mate with alternatives.

Plaistow et al. (2004) concluded that distinguishing between conditional and pure strategists in populations is complex. Also, their model shows that conditional and pure strategies are not necessarily mutually exclusive and can possibly co-exist in the same population of individuals, since a pure conditional equilibrium is only feasible in the absence of costs or limits to conditionality. On the other hand, pure strategies involving genetic polymorphisms may include a conditional strategy in which one of the tactics is extremely rare and may thus be mistaken for a fixed strategy.

3. Competition, cooperation and the evolution of female coalitions in matrilineal social formations

3.1 Competitive and cooperative relationships

So far I have discussed direct competition over reproduction, however, the nature of competitive relationships changes considerably when animals live in groups, since individuals depend on their cooperative relationships with other individuals. Typical examples of cooperation include warning calls, collective defence of home range against predators, food sharing, mutual tolerance around feeding sites, and the formation of alliances (Walters and Seyfarth, 1987). However, due to the close proximity of group-living animals, conflict over access to resources is bound to arise. Direct competition in social interactions is usually (but not always) reflected in

aggressive behaviour, which can manifest itself in several contexts including competition over food or mates, or for the establishment and maintenance of dominance rank. However, the negotiation of resources does not usually take place in repeated fights, but rather by the expression of ritualised displays and relationships of dominance and submission that rarely lead to physical violence, but often determine which individuals gain access to resources (e.g. Primates: Walters and Seyfarth, 1987).

3.2 Dominance hierarchies

When individuals encounter each other regularly, repeated competitive interactions can occur. When these interactions result in consistent 'winners' and 'losers', it is possible that these animals live in dominance hierarchies with clear differentiated relationships. Lehner (1996) proposed a method for constructing dominance hierarchies, which involves presenting the data from several interactions in matrices that summarise the pattern of win-lose interactions between each pair of individuals. Resource holding potential (Maynard-Smith and Parker, 1976) was initially proposed to predict which individuals are likely to win physical contests, which is often based on physical attributes such as body size (Renision, 2002; Lindström and Pampoulie, 2005). Various dominance hierarchies have been constructed based on the outcomes of dyadic encounters, ranging from a strict linear formation to a weak hierarchical organization (see review: Lazarus, 1982). It is difficult to assess however, how animals maintain stable linear or near-linear hierarchies based on fighting ability, especially when the differences in individual fighting ability are small and thus the outcomes unpredictable.

3.3 Matrilineal dominance hierarchies

Following the critical writings of female primatologists, such as Donna Haraway (Primate Visions: 1989) and Sarah Blaffer-Hrdy (The Woman that Never Evolved: 1981), the field of primatology has had a profound influence on the way science views and depicts females and their relationships. Nowadays a vast amount of evidence exists, which supports the idea that the success of many primate societies hinges upon female relationships and organisation, rather than male control. In fact, in 81% of diurnal non-human primates, females are gregarious (see Sterck et al., 1997). Female bonds in the form of coalitions or alliances often allow females to dominate males that are larger and

stronger, even in patriarchal societies (Parish, 1996). For example, in sexually dimorphic primates such as vervets, in which females are smaller than males, females often attack males in coalitions both in feeding and non-feeding contexts (Cheney, 1983).

Several cercopithecine primates, including macaques, baboons and vervets, form strictly linear dominance hierarchies, where related individuals tend to occupy adjacent ranks (Gouzoules and Gouzoules, 1987). In these matrilineal societies, females form the core of the social group, and daughters acquire a social rank just below their mothers (with the youngest always ranking directly below their mother). Matrilineal systems are common in many old world primates and female spotted hyenas, in which high rank is usually associated with reproductive benefits due to reduced inter-birth intervals, reduced mortality during times of food shortage, and increased offspring survival (Silk, 1987).

3.4 The ontogeny of social rank

In matrilineal systems, the acquisition and maintenance of social rank are based on social conventions rather than the ability to win contests (though occasionally this can determine rank reversals). Thus, female dominance differs from many of the dominance patterns observed in males, since it rarely depends on attributes such as size, strength and agility (Walters and Seyfarth, 1987). For example, it is not rare to observe a spotted hyena cub dominating a fully-grown adult female or male (personal observation). Mothers often support their daughters in social interactions. However, juveniles also gradually learn by themselves how to communicate their dominance and subordinate status in relation to others, partly by observing interactions between their mother and other females. Here, it presumably becomes clear to juveniles, which females are dominant and/or subordinate. Also, adult females may signal their social status either by behaving aggressively towards juveniles, or by expressing appeasement behaviours (Walters and Seyfarth, 1987).

3.5 The acquisition and maintenance of social rank: coalitions and alliances

Once reaching adulthood, the acquisition and maintenance of dominance rank depends

on support from individuals other than their mothers (e.g. rhesus monkeys: Chapais, 1983). Aspects of social organisation including female philopatry, and matrilineal hierarchies with well-differentiated relationships, are expected to promote the formation of female coalitions and alliances (Silk et al., 2004). Also, when ecological conditions favour the collective defence of resources, it is predicted that individuals should invest in social relationships that provide coalitionary support (Silk et al., 2004). In cercopithecine primates, where females usually remain together, grooming and alliances are common between kin and non-related individuals (see reviews: Chapais, 2001; Silk, 2002). Coalitions are complex, because they are usually based on a combination of cooperative and competitive behaviours. For example, coalitions can be used for group defence, the defence of carcasses against other predators, defence of young, allo-suckling and group hunting (East and Hofer, 2002); but are also important for the acquisition and maintenance of social rank, as is the case in many cercopithecine primates (Cheney, 1977; Seyfarth, 1977; Harcourt, 1992; Chapais, 1992), and spotted hyenas (Mills, 1990; Zabel et al., 1992; East et al., 1993; Smale et al., 1993; Jenks et al., 1995; East and Hofer, 2001).

Kin selection, reciprocal altruism, and individual benefits have all been proposed to explain the pattern of coalition formations (see summary of these hypotheses in Table 2; taken from Silk et al., 2004). In cercopithecine primates (Silk et al., 2004) and spotted-hyenas (see Chapter 6), it appears that individuals try to maintain their social status by associating mainly with adjacent individuals in the dominance hierarchy, and rarely challenge higher-ranking females, which as a consequence stabilises the dominance hierarchy and maintains the status quo.

Table 2. Hypotheses and predictions for coalition formations (Silk et al., 2004)

Hypotheses	Predictions
Kin selection favours intervention	Females support close maternal kin more than distant maternal kin
	Females support distant maternal kin more than 'nonrelatives'
Reciprocal altruism favours intervention	Females selectively support unrelated females who support them
	Females selectively support unrelated females who groom them
	Females establish stable alliances with particular partners
Individual benefits favour intervention	High-ranking females intervene more frequently than low-ranking females
	Females support subordinate females more often than they support dominant females
	Females intervene on behalf of the higher-ranking of two contestants (conservative support)
	High-ranking females are more conservative in their intervention behaviour than low-ranking females

Conversely, in those species where females do not form strong social bonds, alliances are likely to be less common. For example, female gorillas usually disperse from their natal group and thus grooming and the formation of alliances is far less frequent. Therefore, this indicates that social structure is one important determinant of the pattern of cooperative behaviour in primates (Walters and Seyfarth, 1987). However, what influences the formation of female relationships, and why do some females live in close-knit societies while others are more diffuse?

4. Ecological influences on female social behaviour and group structure

It has been suggested that ecological variables influence the spatial and temporal distribution of females, while male distribution depends on the location of females (Lindenfors et al., 2004). This is based on the prediction that resources and predation

account for variation in female reproductive success, whereas access to females determines reproductive success in males (see Lindenfors et al., 2004). In their comparative study, Lindenfors et al. (2004) reinforced previous findings that show that male and female group sizes are strongly correlated across the primates. Their results also revealed that changes in the number of males lagged behind the number of females. Taken together, these findings support the hypothesis that females drive social evolution in primates, in which females adjust their group size to ecological variation, followed by males who adjust their spatial-temporal distribution to that of females.

In this section, I focus on the huge variety of female social formations in primates, and the way they are influenced by social and ecological circumstances. Feeding competition has a huge influence on female social organisation, and is thought to predict when females should disperse or remain in their natal group (Wrangham, 1980). This is also known as the Ecological model, which focuses specifically on ecological factors in the evolution of female social relationships. The first assumption of the model is that female sociality is necessary for coping with predation in diurnal primates, and second, that female gregariousness results in feeding competition amongst females (Sterck et al., 1997). For example, in mountain gorillas, in which food is abundant and evenly distributed, females disperse from their natal group and rarely interact with female kin as adults (Stewart and Harcourt, 1987). Conversely, in the squirrel monkey (*Saimiri sciurius*), within group food competition is high, and these animals demonstrate differentiated female relationships, female philopatry and a female dominance hierarchy (Mitchell et al., 1991). Interestingly, in a close relative: the squirrel monkey *Saimiri oerstedi*, within group competition is low and females do not form dominance hierarchies and disperse from their natal group (Mitchell et al., 1991).

This latter example provides strong evidence that food distribution plays an important role in the structuring of female relationships. Furthermore, female dominance itself may also evolve as a consequence of ecological circumstances. In the ring-tailed lemur (*Lemur catta*) for instance, males appear to be predisposed to submit actively to females, or in response to female aggression, at the onset of the breeding season. It is hypothesised that female dominance in this species evolved as a consequence of reproductive seasonality and seasonal resource availability. Such female synchronisation in reproduction means that females simultaneously experience

increases in resource requirements, and hence higher levels of competition over nutritional resources. Therefore, female dominance may help to reduce inter-individual competition between females and males when female-female competition is high (Sauther et al, 1999). Despite these striking patterns between female social formations and ecological conditions, female organisation also appears to have a phylogenetic component. For example, in most cercopithecine primates social organisation appears to be strongly conserved, despite ecological variability (Di Fiore and Rendall, 1994; Pruetz and Isbell, 2000).

In conclusion, many female primates adjust their social behaviour in response to ecological conditions and competition with other individuals. Although I have so far only reviewed female bonded-societies in primates, later on when I explore female relationships in spotted hyenas many striking similarities will become evident. For example, like many cercopithecine primates, spotted hyenas form matrilineal dominance hierarchies and female alliances, which are important for the acquisition and maintenance of social rank.

Chapter 4. *The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae)*

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G. Raihani: collected the data used in the study, manuscript writing (50%)

T. Székely: suggestions to improve the manuscript, general editing of the manuscript (15%)

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C. Pitra: provided the phylogeny, suggestions to improve the manuscript (10%)

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Abstract

Bustards exhibit an exceptional variation in sexual size dimorphism (SSD) among birds ranging from reversed dimorphic species (i.e. male < female) through monomorphic species to species in which an adult male can be three times heavier than an adult female. We use this unusual interspecific variation to test functional hypotheses of SSD using phylogenetic comparative methods. We show that bustards exhibit a strong allometric relationship between SSD and body size that is consistent with Rensch's rule. Then we test whether the intensity of mating competition and the agility of male displays relate to SSD. First, the intensity of mating competition predicts that male size relative to female should be larger in species in which the males compete intensely for females. As predicted, evolutionary changes toward a more polygynous mating system were associated with increases in male body size relative to females. Second, our results are also consistent with the aerial agility hypothesis since in agile bustards the males tend to be smaller relative to females, whereas in non-agile bustards the males are usually larger than the females. We also show that these two types of sexual selection have independent and statistically significant influences on SSD. We conclude that SSD in bustards is most consistent with sexual selection, and influenced by both the intensity of sexual selection and the agility of male displays. Other hypotheses, however, such as fertility selection acting on females and different niche-utilisation of sexes, remain untested.

Key words: Sexual size dimorphism, Otididae, mating system, display behaviour, sexual selection, aerial agility.

1. Introduction

Sexual size dimorphism (SSD) is one of the most conspicuous differences between the sexes. Several functional hypotheses have been proposed to explain SSD (reviewed by Hedrick and Temeles, 1989; Shine, 1989; Andersson, 1994). First, directional selection acting on males (or on females) may select for sexual size dimorphism. Sexual selection via male-male competition or female choice, favours large male size in several birds and mammals (Webster, 1992; Mitani et al., 1996; Dunn et al., 2001; McElligott et al., 2001; Lindenfors et al., 2003). Thus, an increase in body size may be particularly advantageous to males in polygynous species (Clutton-Brock and Harvey, 1977; Owens and Hartley, 1998), since the intensity of sexual selection is greater due to increased competition between males over females.

Second, the direction of sexual selection on body size may also depend on whether the contest is taking place on the ground or in the air (Payne, 1984; Jehl and Murray, 1986; Figuerola, 1999). For example, small and agile males may have an advantage in contest competitions that take place in the air (Andersson and Norberg, 1981), and females also prefer small acrobatic males to large (or less acrobatic) males in raptors and shorebirds (Hakkarainen et al., 1996; Grønstøl, 1996; Blomqvist et al., 1997; Figuerola, 1999).

Third, disruptive selection may influence the body sizes of males and females toward different evolutionary optima. For instance, if males and females compete for resources, then each sex may benefit from avoiding extensive overlap with the other ('different niche utilization', Selander, 1966; Shine, 1989; Thom et al., 2004). However, it is difficult to distinguish whether differential niche utilization is cause or consequence of SSD. Thus, it has been suggested that the exploitation of different resources may help maintain SSD, although it is unlikely to be the driving force behind it (Thom et al., 2004). Recent comparative studies have adopted a broad approach by investigating the influences of both sexual selection and ecological processes on SSD (Figuerola, 1999; Székely et al., 2000; Perez-Barbeíra et al., 2002).

Many animal taxa exhibit an allometric relationship between body size and the extent of SSD across species (Rensch, 1960). This relationship, termed 'Rensch's rule' (Fairbairn, 1997; Abouheif and Fairbairn, 1997), states that among closely related taxa

SSD increases with body size in those species in which the male is larger than the female, whereas SSD decreases with size in species in which the female is the larger sex. A recent genetic simulation model suggests that SSD may change rapidly in response to divergent selection pressures without significant long-term change in the genetic correlation between the sexes (Reeve and Fairbairn, 2001).

Bustards (Otididae) are an excellent group to investigate SSD (Dale, 1992), since they exhibit one of the largest size dimorphisms in any avian taxa. In addition, they include species that have male-biased (e.g. Great Bustard, *Otis tarda*) and female-biased dimorphism (e.g. Lesser Florican, *Sypheotides indica*). Their mating behaviour ranges from socially monogamous to lek breeding. In the lek-breeding Great Bustard large males gain about 30 % in body mass at the on-set of the mating season which suggests that large body mass enhances mating success (Carranza and Hidalgo-Trucios, 1993), although the large body mass at the beginning of the mating season may also allow males to store reserves for the period of intensive displays. Also, males exhibit an unusual range of display behaviour from spectacular ground displays by male Great Bustards to highly acrobatic displays of Red-crested Bustards (*Lophotis ruficrista*). Finally, a recent molecular phylogeny provides a phylogenetic framework for comparative analyses (Pitra et al., 2002).

We have two objectives in this study. First, to test whether SSD relates to body size in bustards as expected from Rensch's rule. Second, we test two mutually non-exclusive functional hypotheses of SSD. On the one hand, the intensity of mating competition hypothesis predicts that male size should be larger relative to female size in species in which males compete intensely for females. On the other hand, the display agility hypothesis predicts that in species with aerial displays male size should be smaller relative to females than in species with non-agile male displays, since smaller body size is assumed to enhance agility.

Phylogenetic comparative methods are often used to test functional hypotheses of SSD (Owens and Hartley, 1998, Szekely et al., 2000, Dunn et al., 2001). These methods are useful for comparing traits across species or taxa within a statistical framework that controls for the effects of common ancestry.

2. Methods

2.1 Data and Phylogeny

We compiled data on body size, mating behaviour and male agility using primary research publications, handbooks and unpublished information (see Appendix 1). Social mating system, a proxy for the intensity of mating competition, was scored as monogamy, territorial polygyny, and lek polygyny. We assume that mating competition increases from monogamy (score 1) to lek polygyny (score 3, see similar scoring by Székely et al., 2000, Dunn et al., 2001). Three species exhibited both territorial polygyny and lekking so these species were scored 2.5 (Appendix 1). Our scores were highly correlated with an independent scoring of mating system (Dale, 1992, $r_s = 0.901$, $P < 0.0001$, $N = 17$ species). Male agility was scored between 1 (low) and 5 (high, Appendix 1). This scoring of male agility is consistent with the approach of Figuerola (1999) and Székely et al. (2000). The score of 1.5 was given when it was uncertain whether male display was 1 or 2 (Appendix 1). The distinctions between scores 1, 1.5 and 2, are ambiguous. Thus we took the advice of an anonymous referee and combined these scores in the analyses. Note that using the original scores (see Appendix 1) does not change our major conclusion.

Initially, we attempted to collect data on body mass of bustards as a further *proxy* for body size. Mass data, however, are subject to daily and seasonal fluctuations (Witter and Cuthill, 1993; Carranza and Hidalgo-Trucios, 1993). In addition, sex specific mass data were available only for few species.

The bustard phylogeny was provided by a recent molecular study (Pitra et al., 2002) that used sequences from mitochondrial cytochrome *b* gene, the noncoding mitochondrial control region II, and an intron-exon crossing fragment of the nuclear chromo-helicase-DNA binding gene. We augmented this phylogeny with two species (Karoo Bustard, *Eupodotis vigorsii* and the Little brown Bustard, *Eupodotis humilis*). The phylogenetic position of the latter two species was provisionally allocated as sister taxa to Rüppell's Bustard (*Eupodotis rueppellii),* because both the Karoo Bustard and the Little brown Bustard were formerly placed in a separate genus (*Heterotetrax*) together with Rüppell's Bustard (Snow, 1978).

2.2 Phylogenetic Comparative Analyses

We used the phylogenetic independent contrasts method of Felsenstein (1985) as implemented by CAIC (Purvis and Rambaut, 1995) to control for phylogenetic non-independence of species. Wing length (in mm) was log_{10} transformed prior to the analyses. An assumption of Felsenstein's method is that standardized contrasts should be independent from their estimated nodal values. We verified this assumption by plotting standardised contrasts against the estimated nodal values for our variables: none of these correlations were statistically significant.

We tested the allometric relationship between male and female body size by fitting major axis regressions (Sokal and Rohlf, 1981) using either the species data or the phylogenetic independent contrasts (Garland et al., 1992). The Rensch's rule predicts that the slope of male: female size should be significantly larger than one. The major axis regression of phylogenetic independent contrasts was forced through the origin (Harvey and Pagel, 1991). We provide the slope of major axis regressions (b) and the 99% confidence intervals (lower CI — upper CI) that were calculated by bootstrapping the contrasts.

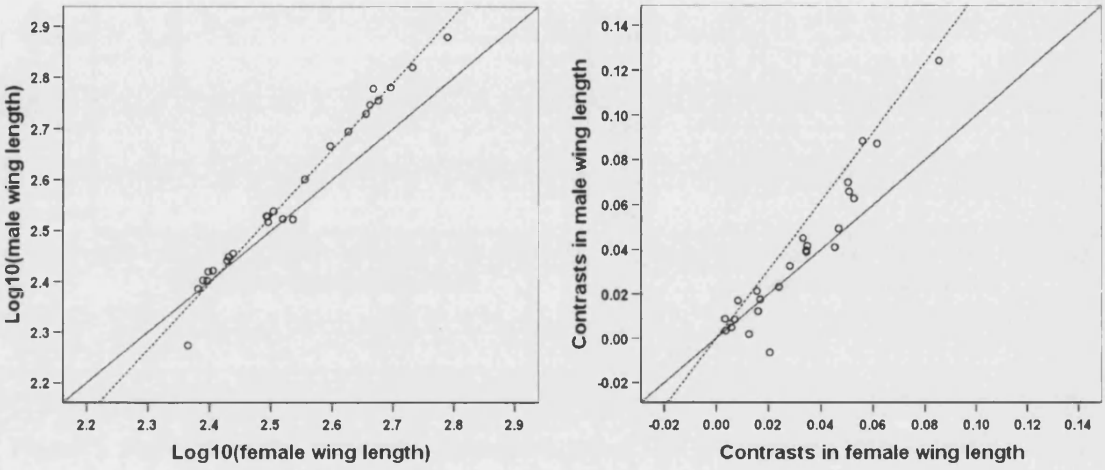
SSD was calculated as contrasts in log_{10}(male wing) – contrasts in log_{10}(female wing). It is customary to use log-transformed data for calculating SSD since the differences between males and females expressed as logarithms provide more accurate estimates of SSD than ratios. In an overview of SSD indices, Smith (1999) concluded that the log-transformed measure is one of only two preferred indices of SSD, since log differences tend to be symmetric around zero, and less likely to violate the assumptions of parametric tests than other indices. Also, log transformation of sizes makes the more reasonable assumption that different lineages are equally likely to make the same proportional change in size (Purvis and Rambaut, 1995). Least squares regressions of contrasts were forced through the origin, since the model predicts the mean value of independent contrasts to be zero (Harvey and Pagel, 1991). We investigated the relationships between SSD (dependent variable), the intensity of mating competition and male agility (independent variables) in bivariate and multivariate least squares regressions. Evolutionary changes in agility and the intensity of mating competition were not related ($r = 0.136$, $P = 0.516$, $N = 24$ contrasts). We also tested the interaction

term between the intensity of sexual selection and male agility (dependent variable: SSD). This interaction was not significant (P = 0.484, N = 24 contrasts) thus we excluded the interaction term from the final multivariate regression model. In the multivariate model we provide the partial correlation coefficient r_p, the significance of r_p and effect sizes (partial eta squared). We used SPSS (Ver. 11.00) for statistical calculations, except that bootsrapping of confidence intervals for major axis regression was carried out in R (R Development Core Team, http://www.R-project.org).

3. Results

3.1 Rensch's rule

Our results are consistent with Rensch's rule since male-biased SSD is greater in large bustards than in small ones (b = 1.311, N = 25 species; Figure 1a) and the 99% confidence intervals do not include one (1.204 — 1.430, N = 25 species). These results remained statistically significant by using phylogenetically independent contrasts (b = 1.542, 1.218 — 1.846, N = 24 contrasts; Figure 1b).



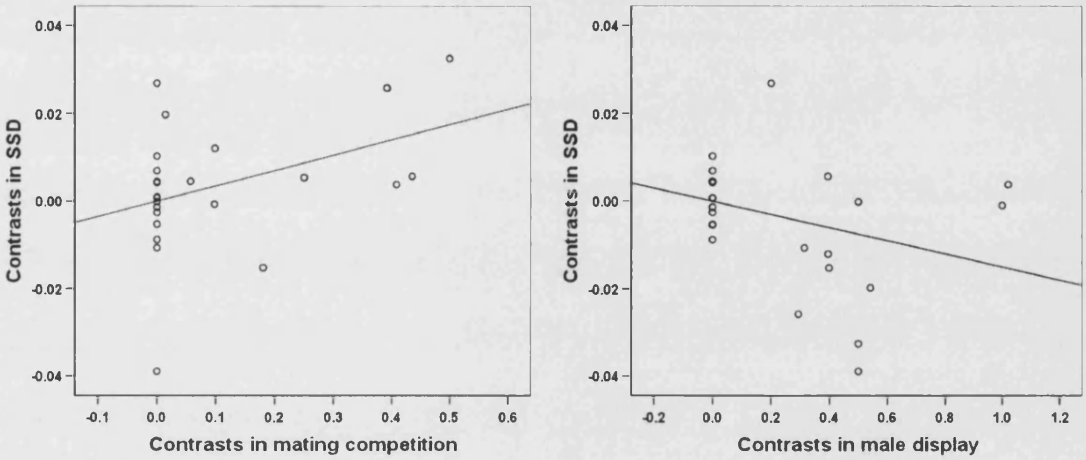
(a) (b)

Figure 1. Rensch's rule in bustards. The continuous line indicates the isometric relationship, and the dotted line represents the fitted relationship between male size and female size by major axis regression for (a) species (b = 1.311, 99% CIs: 1.204 — 1.430, N = 25 species), and (b) phylogenetic contrasts (b = 1.542, 99% CIs: 1.218 — 1.846, N = 24 contrasts).

3.2 Intensity of mating competition and male agility

Evolutionary changes in SSD are positively correlated with changes in the intensity of mating competition (r = 0.453, $F_{(1,23)}$ = 5.934, P = 0.023; Figure 2a). Since the contrasts were highly variable around zero, we repeated the analysis by excluding zero contrasts (see a similar approach by Owens and Hartley, 1998). Nevertheless, the relationship remained significant (r = 0.645, $F_{(1,9)}$ = 6.395, P = 0.032).

Evolutionary changes toward agile displays are also correlated with changes toward small male size relative to females (r = -0.409, $F_{(1,23)}$ = 4.634, P = 0.042; Fig 2b). The strength of the relationship remains after excluding zero contrasts, although the relationship is not significant statistically (r = -0.424, $F_{(1,11)}$ = 2.413, P = 0.149).



(a) (b)

Figure 2. Phylogenetically independent contrasts in sexual size dimorphism (SSD) and (a) the intensity of mating competition (r = 0.453, $F_{(1,23)}$ = 5.934, P = 0.023), and (b) male agility (r = -0.409, $F_{(1,23)}$ = 4.634, P = 0.042). Regressions were forced through the origin.

In the multivariate model of SSD (r^2 = 0.431, $F_{(2, 22)}$ = 8.342, P = 0.002) both the intensity of mating competition and male agility were associated with SSD. Evolutionary changes toward larger males than females were associated with both intensified mating competition (r_p = 0.563, $F_{(1, 22)}$ = 10.197, P = 0.004) and reduced agility of male displays (r_p = -0.533, $F_{(1, 22)}$ = 8.749, P = 0.007). Effect sizes of mating competition and display behaviour were partial-eta squared = 0.317 and partial-eta squared = 0.285, respectively.

4. Discussion

Our study confirms Rensch's rule in bustards (Payne, 1984) and adds to a growing number of taxa in which the rule has been shown including mites, lizards, hummingbirds and shorebirds (Abouheif and Fairbairn, 1997; Cullum, 1998; Colwell, 2000; Székely et al., 2004). In a recent work Székely et al., (2004) have shown that the rule is driven by the interaction between mating competition and male display behaviour. In bustards, however, this interaction was not significant (P = 0.484). We suggest that the latter result may be due to the small number of bustard species that limits the statistical power of models. Note however, that the predictive power of multivariate models was comparable between bustards (r^2 = 0.431) and shorebirds (r^2 = 0.454 - 0.476; Székely et al., 2004).

The relationship between mating competition and SSD is consistent with the hypothesis that sexual selection is responsible for the large body size in males of polygynous species. This relationship has been reported in New World blackbirds (Icteridae), shorebirds (Charadrii) and across a wide range of other avian taxa (Webster, 1992; Székely et al., 2000; Dunn et al., 2001). Thus, male-male competition and female choice may lead to an evolutionary increase in overall body size. Fertility selection is unlikely to explain SSD given that most bustard species lay only small clutches of 1-2 eggs (Collar, 1996).

Our results are also consistent with the aerial agility hypothesis. Interestingly, the influence of agility was comparable to that of mating competition, as indicated by partial effect sizes. Sexual selection will favour small male body size in those species that exhibit aerial displays (Andersson and Norberg, 1981; Jehl and Murray, 1986). This relationship has also been reported in non-polyandrous shorebirds with reversed SSD, showing a significant reduction in male body size from less acrobatic to more acrobatic displays (Figuerola, 1999; Székely et al., 2000). Evidence that females prefer small males has also been shown in Moorhens (*Gallinula chloropus*) and fruitflies (*Drosophila subobscura*, Petrie, 1983; Steele and Partridge, 1988).

Future work may expand our study by investigating other morphological traits that relate to body size, for instance body mass and tarsus length. Also, bustard populations appear to have different body sizes thus comparing populations may be a fruitful approach. In addition, work is needed to quantify their ecology, mating and display behaviours. Bustards deserve more attention since most species are threatened, some even facing extinction in the near future.

Various selective pressures may act on body sizes of females and males. For instance, in most bustards the incubation of eggs and rearing of young is left entirely to the female (Collar, 1996). This may select for smaller body size in females, since they would be better covered by vegetation during incubation and less conspicuous to predators. Large size, however, may allow the sexes to accumulate fat and buffer them against fluctuations in food resources. Thus if one sex forages in a more variable environment than the other, the sexes may have different optimal body sizes.

The type of plumage may amplify display behaviour and thus play a significant part in the evolution of SSD. Display behaviour appears to correlate with male colouration in bustards, since species with aerial displays have more melanised plumage (Dale and Joy, personal communication). The latter result is consistent with the findings of Bókony et al. (2003), who showed that more melanistic shorebirds have more agile displays. Thus, a further implication of aerial displays in males is to enhance the conspicuousness of the plumage in the light background of the sky.

In conclusion, our study shows that SSD in bustards is consistent with Rensch's rule. Our results also support the sexual selection hypothesis so that directional selection may either increase or decrease body size of males; depending on the particular mating strategy and display type.

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Appendix 1.

Data sources and references. The numbers of individuals (males and females) measured for each species are given in the brackets. Mean wing lengths were calculated using the unpublished measurements of Paul Goriup and Patrick Osborne, where indicated. Social mating system and display behaviour were scored by Paul Goriup using his extensive unpublished notes and observations. Mating system was scored as monogamous (MG), territorial polygyny (PG) and lek polygyny (LEK). Display type was scored as (1) ground display with vocalisation only and/or erect neck display; (2) ground display with standing balloon and reverse the plumage; (3) ground display with running and perhaps occasional leaps in the air; (4) aerial non-acrobatic display of high flying; (5) aerial acrobatic rocket display (see Johnsgard 1991). Note that display scores 1, 1.5 and 2 were combined in statistical analyses (see Methods).

Species	Male wing	Female wing	Mating System	Display Type	Reference
	in mm	in mm			
Afrotis afra	281.0 (47)	270.0 (23)	PG	4	4
Afrotis afraoides	285.6 (18)	274.5 (13)	PG	5	1
Ardeotis arabs	604.0 (7)	496.7 (6)	PG	2	1
Ardeotis australis	569.0 (6)	474.0 (12)	PG	2	3
Ardeotis kori	758.0 (36)	616.0 (46)	PG	2	5
Ardeotis nigriceps	661.2 (12)	539.5 (11)	PG	2	1
Chlamydotis undulata	399.2 (25)	359.2 (26)	PG	3	1
Eupodotis caerulescens	333.5 (8)	330.8 (4)	MG	1	1
Eupodotis humilis	252.6 (10)	245.1 (8)	MG	1	1
Eupodotis rueppellii	329.0 (18)	313.0 (13)	MG	1	4
Eupodotis senegalensis	276.1 (14)	268.5 (4)	MG	1	1
Eupodotis vigorsii	337.4 (5)	312.3 (7)	MG	1	1
Houbaropsis bengalensis	333.0 (15)	343.4 (14)	PG	4	1
Lissotis hartlaubii	337.8 (10)	310.8 (6)	PG/LEK	1	1
Lissotis melanogaster	345.5 (26)	319.3 (23)	PG/LEK	4	1
Lophotis gindiana	262.8 (18)	250.1 (12)	PG	5	1
Lophotis ruficrista	263.9 (12)	254.5 (11)	PG	5	1
Lophotis savilei	243.0 (9)	240.8 (4)	PG	5	1
Neotis denhami	558.0 (11)	459.0 (7)	PG/LEK	2	5
Neotis heuglinii	495.0 (3)	423.0 (4)	PG	1.5	2
Neotis ludwigii	536 (6)	452 (5)	PG	1	4
Species	Male wing	Female wing	Mating System	Display Type	Reference
Neotis nuba	463.5 (2)	395.0 (4)	PG	1.5	4
Otis tarda	600.1 (12)	464.8 (10)	LEK	2	1
Sypheotides indica	187.8 (12)	231.7 (11)	PG	5	1
Tetrax tetrax	252.0 (29)	249.0 (15)	PG	4	2

References: (1) Goriup P.D., and Osborne, P.E. (data compilers); (2) Johnsgard, 1991; (3) Marchant and Higgins, 1993; (4) Urban et al., 1986; (5) Percy FitzPatrick Institute of African Ornithology: http://web.uct.ac.za/depts/fitzpatrick/docs/fam31.htm

Chapter 5. *Male mating tactics in the American rubyspot damselfly: territoriality, non-territoriality and switching behaviour*

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Manuscript in review

Details and extent of the contributions by authors

G. Raihani: Collection of data, manuscript writing (50%)

M.A. Serrano-Meneses: Collection of data, statistical analyses (30%)

A. Córdoba-Aguilar: General editing of manuscript, partially wrote discussion (20%)

Abstract

Odonates exhibit a wide range of territorial and non-territorial mating tactics and are ideal for investigating alternative reproductive behaviours (ARBs). We studied male mating tactics in the American rubyspot damselfly (*Hetaerina americana*), in which males are larger than females, and exhibit red wing spots, which have been suggested to have evolved as a consequence of male-male contests. In this species mating success is greatly enhanced by their ability to defend territories along streams and rivers, which in turn depends on the amount of fat thoracic reserves available. Previous studies on this species have distinguished between territorial and non-territorial males, in which the former obtains significantly more matings than the latter. In our study however, we found a third reproductive tactic: switching. These males exhibit both territorial and non-territorial tactics and there was no significant difference in the mating success between the three alternative reproductive tactics. Territorial males contained the higher fat reserves, non-territorial males had the least fat content while the fat load in switchers lay between the territorial and non-territorial tactic. Interestingly, switchers survived for longer and were able to defend territories for more days compared to territorial males. Our results suggest that territorial behaviour is extremely plastic in this species. Finally, we discuss the implications of our study and directions for future work on territorial and non-territorial reproductive tactics in odonates.

Keywords: Sexual selection, alternative reproductive behaviours, territoriality

1. Introduction

The concept of territoriality in animal behaviour was initially inspired by observations in birds, and is broadly defined as 'any defended area' (Noble, 1939, p. 267). Since then, territorial behaviour has been described in a variety of species belonging to different taxa. For example, some animals defend group territories, such as spotted hyenas, that form clans with dominance hierarchies (*Crocuta crocuta*; Kruuk, 1972), and the cooperatively breeding meerkat (*Suricata suricatta*), in which non-breeding animals help to rear offspring (Doolan and MacDonald, 1996). Alternatively, animals also establish individual territories, which may function as a spacing mechanism and/or to increase the ability of individuals to access resources. Some of the best studied cases of territorial behaviour are those in which defended places provide more mating opportunities (e.g. *Plathemis lydia*; Koenig and Albano, 1985; *Anolis sagrei*: Tokarz, 1998).

In the case of territorial species, an individual's ability to obtain and sustain a territory is usually linked to mating success (Andersson, 1994). Not all individuals, however, are able to obtain a territory. This is usually the case in territorial odonates (damsel- and dragonflies) (Corbet, 1999), in which a number of individuals follow alternative reproductive behaviours (ARBs) to have access to females (e.g. Waage, 1973; Forsyth and Montgomerie, 1987; Plaistow and Siva-Jothy, 1996). Non-territorial males, for instance, follow "the best of a bad job" strategy, since, despite their disadvantage, males are still gaining some sexual benefits (Forsyth and Montgomerie, 1987). There is increasing evidence that territorial and non-territorial behaviours are not fixed traits, but rather, different reproductive behaviours or tactics, which males use to enhance their reproductive possibilities (Austad, 1984; Dominey, 1984; Taborsky, 1994; Gross, 1996).

A variety of ARBs appear to have arisen in response to frequency- and status-dependent selection (Gross, 1996). Frequency dependent ARBs are typically described as mixed evolutionarily stable strategies (ESS) (Maynard-Smith, 1982), which assume that at certain frequencies, the relative fitness of coexisting ARBs in a population are more or less equal. However, the tactic that an individual adopts may also depend upon some aspects of its condition (environmental or physiological) (Dawkins, 1980; Gross, 1996),

such as age, size etc. Conditional strategies are most likely to exist in populations where not only those males with the highest levels of competitive ability are able to obtain mates, since conditional individuals are unlikely to reach the same level of competitive ability that pure territorial males use to obtain territories (Plaistow et al., 2004). Therefore, ARBs provide a different framework for understanding adaptive processes, since they give rise to wide phenotypic diversity rather than producing a single best male or female phenotype (Gross, 1996).

Odonates are ideal for the study of ARBs since they exhibit a wide range of mating tactics (reviewed by Corbet, 1999). For example, in damselflies of the family Calopterygidae, the acquisition of a territory is usually a pre-requisite for males to obtain copulations, and is determined by the outcome of aerial encounters between territory holders and intruders (Córdoba-Aguilar and Cordero Rivera, 2005). Due to the energetic costs of fighting, less competitive non-territorial mating tactics are used as conditional strategies, which provide reduced mating opportunities compared to territorial males (Córdoba-Aguilar and Cordero Rivera, 2005). For example, *Calopteryx maculata* males decline in their ability to maintain a territory after 20 days, after which, males switch to a 'wandering' tactic and try to gain copulations by making brief visits to reproductive sites (Forsyth and Montgomerie, 1987).

Mating opportunities clearly differ between alternative mating tactics. For example, in *Calopteryx splendens*, territorial males gain a disproportionately high number of copulations compared to non-territorial males (Plaistow and Siva-Jothy, 1996). Fat muscular reserves (mediated by how much flight muscle has been produced – the more muscle, the more fat reserves can be accumulated – see Plaistow and Siva-Jothy, 1999) is a limiting physiological factor in odonates, which determines whether, and for how long, a male is able to defend a territory (Marden and Waage, 1990; Plaistow and Siva-Jothy, 1996; Koskimäki et al., 2004; Serrano-Meneses et al. in press). Fat is constructed from the food the animal mainly gathers soon after emergence, and is used to fuel aggressive contests (Marden and Waage, 1990; Plaistow and Siva-Jothy, 1996).

Also, as the number of competing males for riverine sites increases, the more energetically expensive fighting for territories will become (Pajunen, 1966). This situation results in territorial males becoming energetically exhausted and therefore,

may lead to them adopting a non-territorial tactic (Plaistow and Siva-Jothy, 1996). Non-territorial males may also be individuals that since the onset of their reproductive life, were not able to manufacture enough fat to gain a territory, and thus remain non-territorial throughout their lifespan (Plaistow and Siva-Jothy, 1996). In a system like this, it would be expected that 'fatter' males devote their energy to defend a territory extensively until they are no longer able to sustain aggressive contests, since the value of the defended resource is very high and re-obtaining a new territory would be energetically costly. Here we explored the territorial and non-territorial tactics in another Calopterygid, the American rubyspot (*Hetaerina americana*). Territorial contests in this species involve males chasing one another in a circular fashion (Johnson, 1963; Grether, 1996b). Once males establish territories, they return to defend the same area each morning until they either die, become displaced (Grether, 1996b) or simply leave the territory. Females visit these breeding sites to copulate with males. After copulation, the male and female fly in tandem to an oviposition site, where females oviposit their eggs under water on submerged plant substrates (Alcock, 1987).

Males of the American rubyspot bear large red spots at the base of each wing. Previous studies have indicated that territorial males are likely to have larger spots compared to non-territorial males in this (Grether, 1996a; Contreras-Garduño et al., 2006; Serrano-Meneses et al., in press) and other Calopterygid species (e.g. Siva-Jothy, 1999; Córdoba-Aguilar, 2002). Wing spots in American rubyspot appear to have evolved in response to male-male competition for mating territories, since males with larger wing spots were able to hold territories for longer and had higher mating success and female choice, at least in the pre-copulatory stage, seems unlikely (Grether, 1996a,b, 1997). The spots may reflect energetic condition as under natural conditions, males with larger spots lived longer compared to males with smaller spots (Grether, 1996a,b). This is congruent with recent results suggesting that spot size is correlated with fat muscular reserves in territorial males (Contreras-Garduño et al., 2006: Serrano-Meneses et al., in press). Furthermore, it was also found that body size and fat reserves influence the ability of males to hold territories and hence their reproductive success (Serrano-Meneses et al., in press). In this study, however, large body size was favoured in territorial males, while small size was favoured in non-territorial males.

In the present work, we studied the nature of the ARBs in this species and correlated these with key aspects that are under sexual selection and reflect male condition: fat reserves, body size, flight muscle and red spots. Unlike other Calopterygid species, including the American rubyspot, we found that a certain set of males exhibit both territorial and non-territorial male mating tactics interchangeably. Here we have called this tactic "switchers". These, as well as "traditional" male mating tactics, are investigated in terms of their fitness payoffs and some hypotheses are put forward to explain their advantages. Our work is novel in the sense that this switching behaviour has not been described before.

2. Methods

2.1 Study site

Fieldwork was carried out in Tehuixtla, Morelos, Mexico (18° 32' 56" N, 99° 16' 23" W, elevation 840 m) from the 17th of December 2003 - 27th of February 2004 (72 days), and from the 24th - 29th of October 2006 (6 days). We worked along the shore of the Amacuzac River in a section approximately 300 m long.

2.2 Marking, body size, morphometrics and age

Animals were caught daily and marked with a unique combination of three digits on the right anterior wing using an indelible black marker. With the use of binoculars, these numbers could be identified from a distance of a few metres; this enabled us to easily identify individuals when carrying out behavioural observations. We measured the body length (from head to tip of abdomen) of each marked male using a digital calliper (to the nearest 0.001 mm). From the 151 individuals marked, we randomly photographed 57 males to determine the amount of wing pigmentation, which was calculated as the proportion of the pigmented area in the wing (see Serrano-Meneses et al., in press for a similar procedure). Photographs were taken at constant distance using a digital camera (Olympus 765UZ). At the time of capture we classified males in one of three age classes: (i) juvenile, (ii) mature and (iii) old. Age was estimated from morphological cues (see Córdoba-Aguilar, 1994): (i) juvenile individuals are brightly coloured with highly transparent and flexible wings; (ii) the colouration of mature individuals is less

bright and intense and the wings are not as transparent and flexible compared to juvenile; (iii) old individuals exhibit dark body colouration, their wings are often damaged at the tips and they are mostly rigid.

2.3 Survival, fighting rate and mating success

During the daily surveys we scanned the study site, identifying as many marked individuals as possible from 1200 to 1400 hrs, and recorded their territorial status (see section 2.4). Territorial males were relatively easy to locate, since they remain in territories, perching on plant substrates that are close to the water. Non-territorial males could usually be found perching on plant substrates further away from the water or in trees above the river. Since non-territorial males are not site-faithful, it was more difficult to locate them, compared to territorial males. However, with the aid of binoculars it was possible to find them either perching in trees or on plants further away from the water. Using these surveys we estimated territory tenure as the number of days a given male was seen defending a territory. Males were classified as defending a territory when they remained faithful to a specific site close to the water, while chasing away males that came within approximately 2 metres of their territory. Similarly, the number of days a male was seen throughout the season (i.e. recorded during the daily surveys) was used as an approximation to survival. When estimating survival we only included those males whose lifetime was fully covered from the study period, and excluded those males that were not marked during the first 15 days of the field season (December 2003 – February 2004). Although still conservative, this provided a more accurate survival estimation.

The fighting rate of males was estimated from behavioural observations that were conducted over a period of 72 days between 1000 and 1500 hrs (Central Standard Time), which is the period when males were most active. 39 males were scan sampled and their behaviour was recorded every 10 seconds for a period of 15 minutes using a digital timer. Typical behavioural categories were i) perch, ii) patrol, iii) chase, iv) fight, and v) copulate (see Serrano-Meneses et al. in press for a similar approach). We then estimated the proportion of time that males spent fighting compared to the total number of recordings. We also recorded whether males copulated during the day and the territorial status of these males (e.g. territorial or non-territorial; see below for a

description of these categories). We used the number of copulations for each male as an indicator of mating success.

2.4 Male status

In addition to the behavioural observations, daily surveys were conducted over a period of 71 days, in which male mating tactics were identified and categorised as either territorial or non-territorial (see below), based on what has been described in other Calopterygids (Córdoba-Aguilar and Cordero Rivera 2005). Territorial males typically defend specific sites, which can range in size from 1-2m^2, and chase away intruding conspecific males that come within approximately 0.5-2m of their territory range. Non-territorial males are not faithful to specific areas, but instead wander along several sections of the river and usually avoid agonistic interactions with territorial males (see Corbet 1999 for a review on territorial and non-territorial behaviour). In addition to the daily surveys, in which territorial status was recorded once per day, we chose an area in the study site stretching approximately 10 m along the riverbank, in which we recorded the territorial status of 12 randomly picked males once every hour from 1100 to 1500 hrs each day for a total of 9 days. This complemented the daily surveys, since it allowed us to observe the more detailed patterns of territory defence in a subset of individual males. The area was scanned for at least 10 minutes to determine the status of a given male and also to record how long a given male remained territorial every day.

2.5 Fat reserves, muscle mass, body and spot size according to ARB

During the 2006 field season, 16 territorial, 16 non-territorial and 13 switcher (see results section for description of this male mating tactic) males were captured in the study site. From these males we measured fat content, body length, flight muscle mass and the proportion of wing pigmentation. Body length and wing pigmentation was estimated using the methods described above. To measure metabolic fat and flight muscle mass, we used the thorax of males since this division of the body contained the majority of fat and flight muscle (Plaistow and Siva-Jothy, 1996; Corbet, 1999). Fat extractions were made following the method described by Marden (1989), in which available fat is measured as the difference between thorax dry weight and thorax weight after fat extraction by petroleum ether (see Marden, 1989 for full details); therefore, fat

load refers to fat weight in grams. Following the fat extraction, the dry, fatless thorax was immersed in 0.2 M potassium hydroxide for 24 hours, in order to digest the flight muscle mass (Plaistow and Siva-Jothy, 1996). To estimate the flight muscle mass, the remaining cuticle was washed in distilled water, dried, and re-weighed. Therefore, muscle mass in grams was calculated as the difference between the weight of the thorax cuticle including muscle and the dry cuticle containing no muscle.

2.6 Statistical analyses

We investigated differences in male body length among the three mating tactics for both seasons using two-way ANOVAs. In these analyses, male tactic (territorial, non-territorial, switcher) and season (2004, 2006) were used as factors. The interaction term tactic * season was not statistically significant ($p = 0.915$); therefore, it was removed from further analyses. We then constructed one Generalised Linear Model (GLM) in order to analyse the relationship between wing pigmentation and body length by considering season and male mating tactic. In this GLM, wing pigmentation was the dependent variable, tactic and season were factors and male body length was a covariate. We tested all pair wise interactions but they were not statistically significant ($p > 0.198$ in all cases), therefore they were removed from the analyses.

Using two GLMs we then investigated the relationships between 1: fat load and body length and 2: muscle mass and body length by considering male tactic (territorial, non-territorial, switcher). In Model 1 fat load was the dependent variable, body length was a covariate and male mating tactic was a factor. The interaction term body length * male mating tactic was not significant ($p = 0.092$), therefore it was removed from further analyses. Further differences between groups were carried out using the least significant difference (LSD) *a posteriori* test. In Model 2 muscle mass was the dependent variable, body length was a covariate and male mating tactic was a factor. The interaction term body length * male tactic was not significant ($p = 0.874$), therefore it was not included in Model 2. Further differences between groups were carried out using the LSD *a posteriori* test.

Data on fighting rate and survival was log_{10} transformed since they were not normally distributed. Data was normally distributed following the log_{10} transformation. Further

specific differences in size between these tactics were tested using the Tukey test. Data on fighting rate and survival were *log* transformed prior to analyses due to the non-normal distribution of the data. Data was normally distributed after the *log* transformation.

To test differences in the number of days males defended an area (territoriality), we used territorial and switcher males (see results section for a description and explanation of this strategy) only since non-territorial males were never seen defending an area. We used *t*-test to investigate the differences. Data on territoriality were *log* transformed prior to analyses since the data was not normally distributed. Data was normally distributed after the *log* transformation. We then constructed a GLM that included territoriality as the dependent variable, male mating tactic (territorial, non-territorial, switcher) as a factor and survival as a covariate. The interaction term tactic * survival was not significant ($p = 0.991$); therefore it was removed from the analyses.

The number of copulations obtained by males across tactics was investigated using Kruskall-Wallis.

Statistical analyses and figures were produced using SPSS ver. 14.

3. Results

3.1 Description of male mating tactics

Of the 742 males and 104 females captured and marked, 148 males that were consistently present during the study period were used in this study. Territorial males (74 in total) typically began defending territories on plant or rock substrates close to the water approximately at 1000 hrs and left in the afternoon approximately at 1600 hrs. Territorial males would usually return to defend the same territory each morning. When a female passed in the vicinity of a male's territory, the male would attempt to grab the female in order to copulate. Only 2 copulation attempts were observed throughout the field season, and 22 successful copulations that led to oviposition. Females were never observed ovipositing in the male's territory, but instead the male and female flew in

tandem to a 'communal' oviposition site, where many females would oviposit their eggs under water on submerged vegetation. In our study one oviposition site was identified.

Territorial males were agonistic towards conspecific males, chasing them away when they approached within 0.5-2 m of their territory. Territorial negotiations or contests took place in the form of aerial interactions. The duration of these territorial contests ranged from approximately 10 seconds to an extremely intensive 20 minutes of chasing and spiralling. During these contests, males would typically chase one another in ascending and descending spirals.

Non-territorial individuals (53 in total) were not attached to a particular site and they were usually chased away when perching in the vicinity of territorial males or when attempting to gain access to their territory. Only 3 males were observed being displaced following an aerial contest. Non-territorial males were often seen perching in the trees above territories or behind territorial males further away from the water. This is because territorial males usually occupy the perch sites that are close to the water (which females visit for mating), and typically chase away potential intruders.

An alternative mating tactic was also observed. From the daily surveys, we observed that 21 individual males switched between territorial and non-territorial tactics up to three times during the study period. These males differed from territorial and non-territorial males because territorial males only switch once from territoriality to non-territoriality (not the other way round) during their lifespan due to energetic reasons. However, switchers are unusual, since they switched from non-territorial behaviour to territorial behaviour (NT>T). Switching was observed in four different ways: 1) NT>T, 2) T>NT>T, 3) NT>T>NT, and 4) T>NT>T>NT. Therefore, these males exhibited a flexible behaviour by switching between territorial and non-territorial mating tactics. We called these males switchers, since they did not show a fixed behaviour during the study period. Also, switchers usually returned to the same territory when re-adopting a territorial tactic ($\chi^2 = 4.571$, $P = 0.033$, df $= 1$, $N = 14$).

Following this finding, we recorded territorial behaviour five times per day for a set of 12 randomly chosen males. These recordings confirmed the switching tactic, since males exhibited differences regarding the amount of time they were seen in a territory

every day. From the males that were recorded every hour from 11:00 – 15:00, two males were seen on average once in the same area and for no more than 1 day, one male was seen on average twice per day in the same territory for a total of six days, four males were seen on average three times per day in the same territory for two-four days, three males seen on average four times per day in the same territory for six-nine days, and two males were seen on average five times per day in the same territory for seven days. Therefore, unlike true territorial males that remained in territories all day (i.e. for at least four hours), other males were partially territorial or non-territorial since they were only observed in a territory for up to three hours per day or less.

3.2 Body size and wing pigmentation

Body length was not significantly different among seasons ($F_{1,186} = 0.002$, $p = 0.966$, $N = 193$; Figure 1) but it was significantly different among male mating tactics ($F_{2,186} = 5.481$, $p = 0.005$, $N = 193$; Figure 1): territorial males were larger than non-territorial males (Tukey test: $p = 0.003$), but they were not significantly larger than switcher males ($p = 0.345$). Switcher males were not significantly larger than non-territorial males ($p = 0.455$).

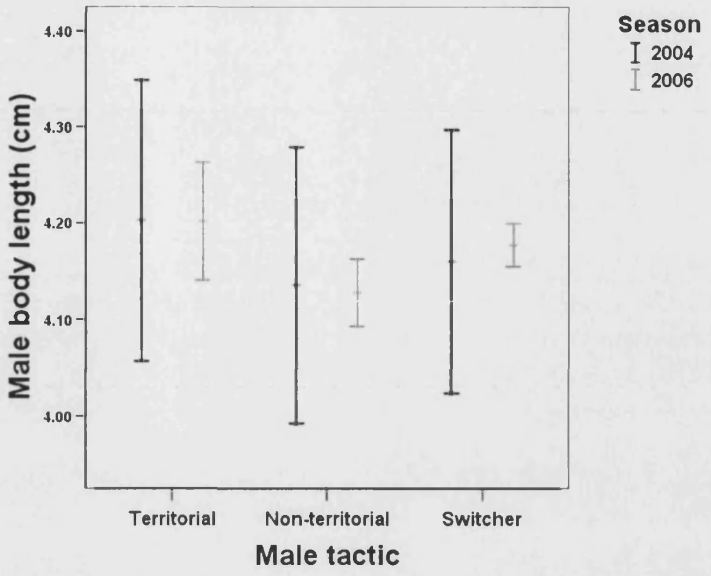


Figure 1. Differences in male body length (cm) between territorial, non-territorial and switcher males and the year in which males were collected. Bars represent means ± S.D.

Wing pigmentation increased with male body length (GLM: $F_{1,93} = 10.070$, $p = 0.002$; Figure 2) and it was different between seasons ($F_{1,93} = 9.977$, $p = 0.002$); nevertheless, wing pigmentation was not significantly different among male mating tactics ($F_{2,93} = 1.028$, $p = 0.362$).

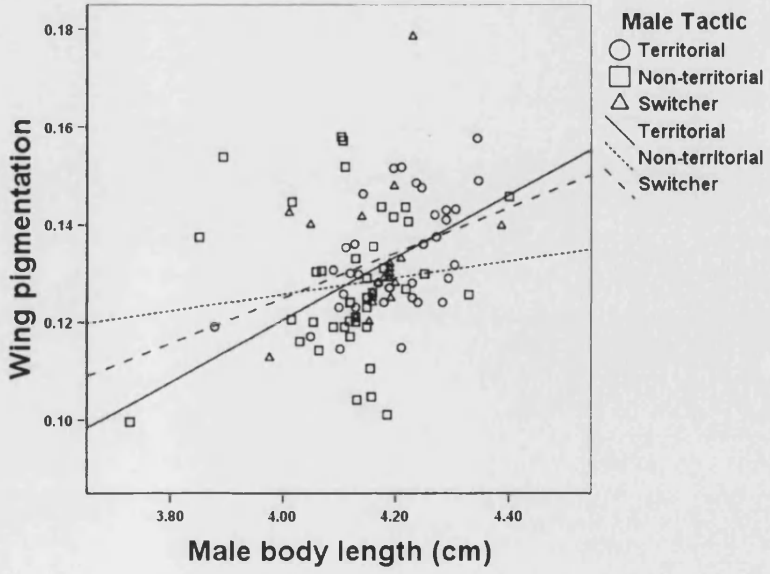
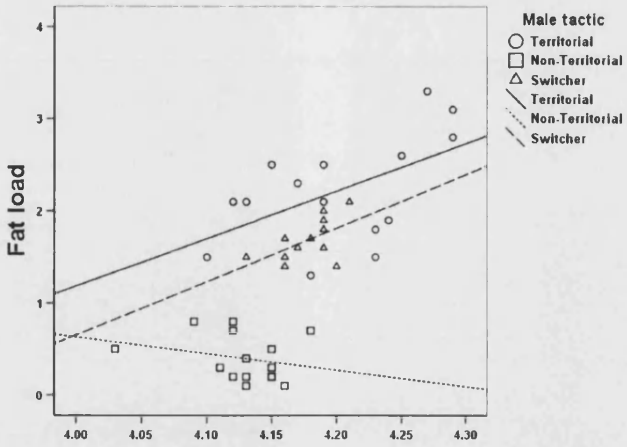


Figure 2. Wing pigmentation in relation to body length in territorial, non-territorial and switcher males

3.3 Fat load and muscle mass

Fat load increased with body length (Model 1: $F_{1,38} = 6.995$, $p = 0.012$), and it was different between male mating tactics ($F_{2,38} = 44.112$, $p = 0.001$; Figure 3a) with territorial males having the highest value followed by the switcher and the non-territorial males respectively (all groups different, LSD test $p < 0.004$ in all cases). Similarly, muscle mass increased with body length (Model 2: $F_{1,38} = 39.183$, $p = 0.001$), and it differed between male tactics ($F_{2,38} = 6.298$, $p = 0.004$; Figure 3b): non-territorial males had more muscle mass than switcher males (LSD test $p = 0.001$), but not significantly more than territorial males ($p = 0.070$). Territorial males did not have more muscle mass than switcher males ($p = 0.102$).

(a)



(b)

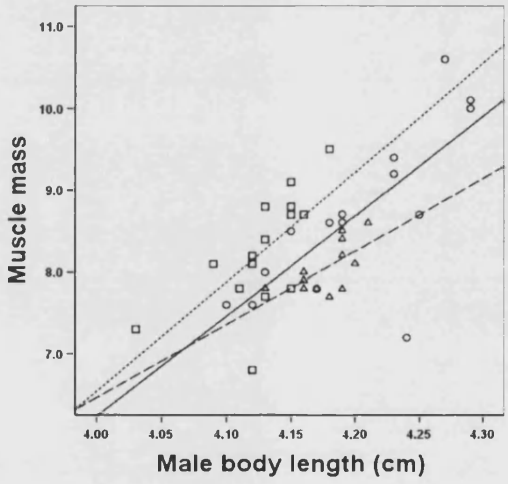


Figure 3. (a) Fat load (g x 10^{-3}), and (b) muscle mass (g x 10^{-3}) in relation to body length in territorial, non–territorial and switcher males.

3.4 Fighting rate, survival and territoriality

There were no significant differences in the fighting rate of the three male mating tactics (one-way ANOVA: $F_{2,36} = 0.722$, $P = 0.493$). However, switcher males appear to spend less time fighting over territories compared to territorial and non-territorial males.

There was a difference in survival between the tactics (one-way ANOVA: $F_{2,142}$ = 12.168, Mean = 0.886, Std. deviation = 0.425, p = 0.001): switchers survived for longer than territorial and non-territorial males (Tukey test: p = 0.001 in both cases); furthermore, there was no difference in survival between territorial and non-territorial males (Tukey test: p = 0.243).

Switcher males were observed defending territories for longer (number of days) than territorial males (t_{77} = 3.056, p = 0.003). Further analyses showed that the number of days a male defended an area increased with survival (GLM: $F_{1,75}$ = 16.957, Mean = 4.77, Std. deviation = 5.864, p = 0.0001). This trend was not different between territorial and switcher males ($F_{1,75}$ = 3.361, p = 0.071).

3.5 Mating success

The number of copulations obtained by males was not different across the different mating tactics (Krukall-Wallis H = 2.880, p = 0.237, n = 15).

4. Discussion

The nature of male mating tactics in Odonata usually occurs as being either conditional- or, more exceptionally, genetically-based (reviewed by Córdoba-Aguilar and Cordero Rivera, 2005). In the former scenario it is possible that those males unable to gather enough dietary resources during either the larval and/or pre-sexually mature stage, are not able defend a territory (Plaistow and Siva-Jothy, 1999). However, those individuals that have secured enough energetic resources previous to sexual maturation start defending territories when sexually mature, and remain territorial until displaced by other males (Marden and Waage, 1990; Plaistow and Siva-Jothy, 1996; Koskimaki et al., 2004). These males are thought to fight until exhaustion presumably because the mating rewards for defending a territory are superior compared to not defending one (Plaistow and Siva-Jothy, 1996). Non-territorial males, however, usually wander through the territories of other males while looking for females, and occasionally gain a few pairings (e.g. Waage, 1973; Plaistow, 1997; Córdoba-Aguilar, 2000). These males, unable to compete with territorial males, do not fight and are usually fat limited in comparison with territory holders (Marden and Waage, 1990; Plaistow and Siva-Jothy,

1996; Koskimaki et al., 2004; Contreras-Garduño et al., 2006; Serrano-Meneses et al., in press). On the other hand, genetically-based strategies are characterised by different phenotypes with two distinct behaviours, in which one male morph shows territorial behaviour while the other adopts a non-territorial option, sneaking for females (Tsubaki, 2003).

In our study we found three different ARBs in American rubyspot males. Two of these are clearly similar to what has been described in other species: territorial and non-territorial males. Territorial males seem to defend a territory until energetic exhaustion while non-territorial males wander through different river localities looking for females. Furthermore, we found a third ARB, which to our knowledge had not been described in the odonate literature, and consists of switching periods of territoriality and non-territoriality by a particular set of males. Switchers were observed defending territories for more days compared to territorial males, which may adopt a non-territorial behaviour once they are defeated after a fight (e.g. Waage, 1973; Plaistow, 1997; Córdoba-Aguilar, 2000). It is likely that defeated males are unable to re-gain a territory because they are energetically exhausted and cannot return to their original energetic values (Plaistow and Siva-Jothy, 1996). This may well be the case for the set of our non-territorial males, which had the lowest fat reserves.

Switcher males however, unlike truly non-territorial individuals, still return to the same place they defended previously, despite leaving for periods of time between territorial defences. The behavioural patterns of switchers were revealed by recording territorial status several times per day. Here we found that the periods of territorial defence during the day are shorter for switchers (three hours or less per day) compared to territorial individuals (four hours or more per day). One possible explanation is that switchers are unable to face long uninterrupted periods of territorial defence due to energetic reasons. Our results support this idea, since switcher males are intermediate in energetic values in relation to territorial and non-territorial individuals. If switching to non-territoriality is influenced by energetics, then the cost of fighting may therefore be higher for switchers, and thus induce them to opt for periods of non-territorial behaviour. During these latter periods it is possible that switchers restore fat reserve limits, although this needs to be corroborated, since it is generally accepted that energetic reserves tend to decrease with adult age once the territorial male has been defeated (Plaistow and Siva-

Jothy, 1996). When analysing the lifetime territorial defence, switching seems to be energetically effective considering that switcher males survived and defended territories for longer, despite fighting at the same rate as the other two male tactics. Furthermore, the number of matings they obtained was similar to territorial and non-territorial males.

The three ARBs also show some other interesting differences. There were differences in body size across the three male tactics with the territorial males being the largest and non-territorial males the smallest. This is in agreement with previous results in this species (Serrano-Meneses et al., in press) and is usually explained by large body size offering more space for flight muscle to be developed after emergence, and consequently, fat reserves (Plaistow and Siva-Jothy, 1999; Matsubara et al., 2005). It is expected that, after the sexual maturation period has been reached, size will be correlated with flight muscle (Plaistow and Siva-Jothy, 1999; Matsubara et al., 2005). This relationship is actually present for the three ARBs as body size correlates with flight muscle. If an animal has a large size with a considerable amount of flight muscle, then it will have more space for the storing of fat reserves. This is why territorial males are larger, and have more fat reserves compared to the other two ARBs. However, as expected, fat is likely to be the main determinant of male-mating tactics, since territorial males and non-territorial males did not differ significantly in their amount of muscle mass. Switcher males show intermediate values of body size, and fat reserves, which suggest that their reduced energetic condition, compared to territorial males, may be the explanation as for why they do not spend all their time defending a territory.

Why do switcher males return to the same territorial spot to defend after some periods of non-territoriality? In general, males of the genus *Hetaerina* do not defend oviposition resources, unlike other Calopterygids (Córdoba-Aguilar and Cordero Rivera, 2005) and territorial odonates in general (Corbet, 1999). Therefore, the quality of a territory, in terms of its oviposition resources cannot be an explanation for choosing a territory in this species (for a similar rationale see Lefevre and Muehter, 2004). In fact, once the couple has been formed, both animals have to locate a place to lay eggs. A system like this resembles that of lekking insect species, in which males exhibit their energetic ability by defending a place, but do not offer nuptial gifts or parental care to females (reviewed by Höglund and Alatalo, 1995). In the American rubyspot, females are usually chased and clasped by males (Grether, 1996b), however, successful copulation

in odonates requires cooperation from the females (Corbet, 1999). Grether (1996b) proposed that larger male size in this species is the product of either male-male competition or intersexual conflict, since large male size may have evolved as a response to resistance by females. However, the evolution of male territoriality may also be driven by female choice, which restricts the location of males to particular areas, since the forcible clasping of females by single or multiple males is more frequent when territorial defence by males is rare (Grether, 1996b). This, along with the fact that it is extremely difficult for males to find females in this species may have influenced the evolution of lekking behaviour in males.

This perspective of a true lek in odonates has not been proposed (except for *Plathemis lydia*, a dragonfly), in which males defend and offer oviposition resources to females (Campanella and Wolf, 1974). However, although the authors proposed a lek system for this species, it remains debateable since lekking males, by definition, do not defend or offer resources to females. In such a system it is assumed that there exists a territorial hierarchy with dominant (i.e. territorial) and subordinate (i.e. non-territorial) males, in which male status has to be validated every time the male returns to its spot. In the case of switcher males, returning to the same place may be paradoxical if a male with high energetic status (at least higher than the returning switcher male) has taken the place during the switcher male's non-territorial period (which may have taken several hours or even days unlike a true territorial male, who is not absent from his territory unless when leaving with a female to oviposit her eggs for some minutes). In a situation like this it may be extremely costly not to choose another place and would imply that there is no communication of energetic status of competing males during fighting.

One alternative explanation is that, given that switchers gain a substantial number of matings (at least similar to territorial individuals), they may benefit by consistently returning to the same place (it has actually been shown that both sexes in this species have a spatial memory when choosing their roosting sites, which last throughout their lifetime; Grether and Switzer, 2000). One potential experiment to test whether switcher males change territories would be to reduce the number of matings or females. Here, the prediction is that switchers should respond to the lack of mating opportunities by changing to another territory, which has been observed in other territorial odonates (Switzer, 1997 a,b). However, a number of matings we observed in switcher males may

have been obtained while these were non-territorial. This and the fact that truly non-territorial individuals also did not differ in their number of matings compared with the other ARBs, suggest that both territoriality and non-territoriality produce equal benefits in reproductive terms. This result is radically different to what has been observed in this (Grether, 1996a,b; but see Serrano-Meneses et al., in press) and other species (reviewed by Córdoba-Aguilar and Cordero Rivera, 2005) in which territorial males gain a disproportionately high number of matings. Due to the fact that previous studies had not identified the switcher behaviour (but was implied by Serrano-Meneses et al., in press), they may have only revealed crude differences in mating number by, for example, inflating the number of matings in truly territorial males, whose set may have included switcher males (with the same being the case for switcher males and non-territorial males).

In summary, our study has revealed a set of three potential ARBs, which can provide similar fitness payoffs: territorial, non-territorial and switcher (individuals with both territorial and non-territorial periods) males. These ARBs are based on physiological, energetically based differences, which may affect the decision of opting for a particular strategy. These results are new in odonates and may call for a re-analysis of reproductive behaviour in other odonate species.

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Chapter 6: *Competition, cooperation and the dynamic structuring of social formations in spotted hyenas*

Gina Raihani

Summary

Hyaenidae comprises four genotypically distinct species that exist throughout Africa and some parts of Asia: The brown hyena (*Hyaena brunnea*), striped hyena (*Hyaena hyaena*) aardwolf (*Proteles cristatus*) and spotted hyena (*Crocuta crocuta*). Although they resemble dogs in appearance, their closest ancestor is considered to be the mongoose. In this Chapter I explore the social structure of spotted hyenas (*Crocuta crocuta*) in the Serengeti National Park Tanzania, and review the different routes to social dominance within this species. Competition over dominance in litters occurs through dyadic aggressive interactions. When animals reach adulthood, the acquisition and maintenance of dominance differs between males and females: Females form coalitions, whereas males observe strict queuing conventions. Finally, I look in detail at how female interactions in coalitions result in the stability of the hierarchy and how alterations in the availability of coalition partners can lead to instability and changes in dominance status for individuals. It has been suggested that female spotted hyenas are anatomically and behaviourally masculinised and more aggressive than males (Mathews, 1939; Glickman et al., 1987; Frank et al., 1990; Zabel et al., 1992); however, others have challenged the hyper aggressive image frequently associated with female spotted hyenas (Goymann et al., 2001a; East and Hofer, 2002; Wilson, 2003), which has been generated by untested assumptions, including the assertion that females are larger and more aggressive than males (Frank et al., 1990).

1. The spotted hyena in culture and science

Before discussing the biology, behaviour and ecology of spotted hyenas, it is important to understand hyena representation in culture and science to show how these have influenced our modern scientific and cultural understanding of these animals.

The 'problem' that hyenas pose for humans is one of gender, which goes back many centuries, crossing cultural boundaries from African folklore to Aristotle. In ancient and still many present societies gender often determines an individual's identity and role in the community. The idea that any human or animal could take the form of both genders simultaneously, or could switch genders, both confused and intrigued the ancient world

(Pendergraft, 1992), and modern science alike. Gender stereotypes are still prominent today, even in many modern western civilisations. For example, the classic Walt Disney production reinforces a male dominant society (Wong, 1999), where males take the role of the 'protectors', are responsible for making decisions, and take the lead to fight and command. It is perhaps not surprising that such cultural preconceptions have led to many biases in the scientific study of spotted hyenas, in which females are the dominant sex and almost indistinguishable from males in appearance. Perhaps the portrayal of hyenas as greedy, deceitful, selfish and stupid in the 'Lion King' reflects an androcentric bias in human societies. Even in scientific journals, spotted hyenas have been described as hyper-aggressive animals that exhibit abnormally high levels of aggression (Frank, 1994: 'When hyenas kill their own').

What has proven most puzzling for ancient cultures and scientists alike is an explanation for the lack of sexual dimorphism in spotted hyenas. Unlike humans and other predators such as lions, telling the difference between males and females is not based on obvious visual cues. Female spotted hyenas have an enlarged external clitoris that is almost identical to the male penis in appearance. It is possible to differentiate between the male and female genitalia only on close inspection, since only the tip of the 'penis' differs slightly between the sexes (Frank et al., 1990).

Since hyenas differ from human-prescribed gender norms, Wilson (2003) argues that hyenas have always operated culturally as a sign of disorder. Stetkevych (in Wilson, 2003) proposes that hyenas pose a category crisis and ultimately a situation in which one transgression (i.e. the gender transgression) leads to misrepresentations in other domains, which together represent spotted hyenas almost as 'anti-culture'. This is perhaps why spotted hyenas embody a range of anti-social attributes. However, when subjected to scientific studies, along with the rise of feminist critiques in biology that challenged implicitly androcentric assumptions of sex and gender, a mixed view of spotted hyenas began to emerge. Hans Kruuk (1972) portrays spotted hyenas as extremely social animals that live together in stable, peaceful societies, and their complex, dynamic social hierarchy enables clan members to manage food competition and avoid conflict. Despite being depicted mainly as scavengers, they are in fact very skilled hunters, where lions frequently scavenge off their kills (Kruuk, 1972). However, others were interested in the internal functions of spotted hyenas and whether there

exists an androgenic basis for the 'masculine' traits observed in females (see Glickman et al., 1987). These studies describe a different picture, in which abnormally high levels of male hormones in female spotted hyenas, compared with other female mammals, cause their apparent "hyper-aggressiveness".

The "androgenised" view of spotted hyenas extends beyond the female phallus, to almost every aspect of spotted hyena biology, behaviour and social life. Because the female extended clitoris looks like a phallus, it is generally viewed as a masculinised trait (Frank, 1995), or a case of sexual mimicry (Muller and Wrangham, 2002). The sexual mimicry hypothesis argues that male mimicry by females may be advantageous to females, since they are more likely than males to be the targets of aggression by other females, particularly at an early age when siblicide and infanticide pose a large threat to infants (Muller and Wrangham, 2002). However, many animals lack sexual dimorphism at the infant stage, since secondary sexual traits often emerge at later stages of their development (Andersson, 1994). Also, support for the sexual mimicry hypothesis requires the investigation into other cues, which may communicate an individual's sex, despite their similarity in appearance. For example, it has been suggested from behavioural evidence that scent marks impart information about the sex, familiarity, and even identity of conspecifics (Drea et al., 2002). Therefore, if scent marking is the most powerful conveyor of information, then male mimicry is unlikely to be as advantageous for concealing the sex of individuals.

Male mimicry by females was proposed as one alternative hypothesis to the idea that circulating androgens in the womb are responsible for producing large and 'androgenised' hyperaggressive females that are able to dominate males (Gould, 1981; Glickman et al., 1993; Frank et al., 1996). However, this hypothesis could no longer be supported after Drea et al. (1998) demonstrated that the female 'penis' still develops in cubs even when circulating androgens are reduced to low levels. Therefore, the structure is not produced, as previously thought, by high levels of androgens, and females should not be termed "androgenised". Another hormone study by Goymann et al. (2001a) revealed that spotted hyenas follow a standard mammalian pattern, with testosterone concentrations in reproductively active males being an order of magnitude higher than in females, and androstenedione levels being similar in both sexes. Unlike previous hormone studies, Goymann et al. (2001a) distinguished between testosterone,

5-α-dihydrotestosterone and androstenedione, and eliminated the possibilities of cross-reactions that could distort the results. No evidence was found to support the previous suggestion by Packer et al. (1995) and Frank et al. (1995), who argued that abnormally high levels of androgens result in hyperaggressive behaviour or pathological problems during reproduction in female spotted hyenas. Furthermore, females are not necessarily larger than male spotted hyenas (Hamilton et al., 1986; East and Hofer, 1997, unpubl. data), nor is body size in males and females related to social rank in the Serengeti clans (East and Hofer, 1997; 2001).

In conclusion, selection for the evolution of large aggressive females is not supported by the current knowledge of behaviour, ecology and endocrinology in this species (East and Hofer, 2002). Also, selection for androgens does not result in the development of the enlarged female clitoris as a by-product of selection.

2. Introduction to the social life of spotted hyenas

Spotted hyenas (*Crocuta crocuta*) are social carnivores that live together in female-dominated clans that defend communal territories (Kruuk, 1972). Females are usually philopatric and clans normally consist of natal adult females and juveniles, and immigrant adult males. Spotted hyenas form matrilineal hierarchies in which offspring usually acquire a social status just below their mother (Smale et al., 1993; Hofer and East, 2003). A matrilineal structure is widespread in social groups of cercopithecine primates including macaques, baboons and vervets (Chapais, 1992), in which females form the central core of the social group (see also Pusey and Packer, 1987). In female spotted hyenas, there is no genetic evidence to suggest that social rank is directly inherited from mothers (East, personal communication), but mothers do usually help their offspring to acquire a dominance status just below themselves (Smale et al., 1993; Hofer and East, 2003).

Social bonds among natal females are stronger than those among adult immigrant males, or between immigrant males and females. In females, coalitions are important for the acquisition and maintenance of social rank, since adult females may dramatically decline in social status following the death of a strong coalition partner such as a mother or adult daughter (Hofer and East, 1996, 2003). However, joining a coalition also entails

risks that may lead to an individual dropping in social rank. There is competition among clan females for access to resources, and this leads to conflict between female clan members. Despite this conflict, female clan members cooperate to defend resources on the territory (East and Hofer, 1991a,b), and the manner in which females initiate greeting ceremonies suggest that social bonds with other female group members are a valuable resource (East and Hofer, 2002). Thus, spotted hyenas have evolved behaviours that resolve conflict (East et al., 1993; Hofer and East, 2000), and hyena society is based on a combination of competitive and cooperative behaviours (East and Hofer, 2002).

Social hierarchies, based on relationships of dominance and submission, become established by the cultivation and maintenance of social bonds. We find these relationships in many species belonging to different groups and taxa, such as the olive baboon *(Papio anubis)* (Barton and Whiten, 1993) spotted hyenas (Kruuk, 1972), mountain goats (Côté, 2000) the dwarf mongoose (*Helogale parvula*) (Rasa, 1987), Arabian babblers (*Turdoides squamiceps*) (Zahavi, 1990) etc. Group living can be beneficial for animals in many ways. For example, the aggregation of adult female hyenas at the communal den helps to protect cubs from potential predators such as lions. Meerkats (*Suricata suricatta)* rely on helpers to rear offspring and guard them at the burrow while others search for food (Clutton-Brock et al. 1998).

Perhaps one of the main benefits of group living in spotted hyenas is a reduction in the pressure of food competition caused by other predators and mortality caused by lions (Höner et al., 2005). Predation by lions poses a significant threat to adult and juvenile spotted hyenas (Kruuk, 1972; Mills, 1990; Hofer and East, 1995), and an increase in lion population size may have led to the decline in numbers of spotted hyenas in the Ngorongoro Crater in the 1970's and 1980's (Höner et al., 2002). However, a group of spotted hyenas can succeed in robbing kills from female lions (Cooper, 1991; Höner et al., 2005), and are well adapted to finding and eating food in a very short time. Predators have evolved a variety of strategies to overcome competition for resources. Cheetahs for instance, hunt during the day instead of night when lions are active, and leopards usually feed on smaller animals that they can carry into trees to prevent kleptoparasitism by lions and hyenas.

It has been suggested that flexible behaviour with regard to territorial conventions permits spotted hyenas to adapt their foraging/ranging behaviour to widely different densities of prey (Hofer and East, 1993a). For example, when comparing the resident herbivore densities in clan territories of the Serengeti National Park, Tanzania, with clan territories in the Ngorongoro Crater, we find a much larger resident herbivore density in the Crater (approx 95 resident animals/km^2: Kruuk, 1972), compared to the Serengeti (approx 3.3 resident animals/ km^2: Hofer and East, 1993a). In the Serengeti, high biomass only occurs in areas containing migratory herbivores. Despite such low numbers of resident herbivores, Serengeti spotted hyenas are able to sustain larger groups because they have evolved a commuting system, which enables individuals to exploit large concentrations of migratory prey outside the clan territory when food availability within their home territory is low.

Commuting is important for Serengeti spotted hyenas because large numbers of migratory prey (219 animals/ km^2: Hofer and East, 1993a) are only present in any specific clan territory for about 30% of the year (East and Hofer, 2002). In this system lower ranking females in the linear hierarchy undertake long distance foraging trips when the abundance of migratory prey in the clan territory is insufficient to feed all members of the clan, but all members must forage outside the clan territory when food abundance is extremely low. Thus, the proportion of commuting animals increases as the density of migratory herbivores declines within the clan territory (Hofer and East, 1995). Therefore, although spotted hyenas are highly social, they also have a fission fusion society, so that members of a clan also operate as individuals, while being part of a social group when necessary. Therefore, when food gets low, spotted hyenas can exploit resources outside the clan territory by commuting (i.e. not a rigid application of territoriality as in lions).

2.1 The male hierarchy

In male spotted hyenas social status follows a queuing system, and increases with a male's length of tenure in the clan (East and Hofer, 2001). Queuing systems have also been reported in other species including many cooperatively breeding birds (Wiley and Rabenold, 1984), and savannah baboons (*Papio cynocephalus*) (Alberts et al., 2003). However, unlike savannah baboons, social status is not a strong predictor of mating

success in male spotted hyenas (East et al, 2003). Immigrant male spotted hyenas rarely use physical contests to improve their social status and male social status is not related to body size. The male queuing system is stabilised by coalitions between adjacently ranked males, which probably helps prevent shorter tenured males from attempting to jump the queue. The social position of top ranking males may also be stabilized by their formation of coalitions with dominant females against other males. In these coalitions top-ranking males may support females that are being harassed by shorter tenured males (East et al., 2003). Thus, coalitions may stabilise the male hierarchy and also strengthen bonds between longer tenured males and females (East and Hofer, 2001). On rare occasions, immigrant males form aggressive coalitions to overthrow longer-tenured males.

It has been proposed that females have control over mating (East et al., 1993), because males need cooperation from females to enable copulation (Kruuk, 1972). Thus, it has been suggested that males need to cultivate relationships with females, which may lead to a lack of physical contests among males (East and Hofer, 2001). Spotted hyena males that develop amicable relationships with females sire more offspring than males that shadow (follow), defend (chase other males away) and harass (creeping up on females and/or biting them) females (East et al., 2003). Females older than 5 years of age tend to be more tolerant towards longer tenured males compared to younger, less experienced males, and young females are more tolerant of recent immigrants (East and Hofer, 2001). This age assortative mating is confirmed by genetic paternity analyses using microsatellite profiling (East et al. 2003). As females mate with multiple males, and even mate with males when they are not in oestrus, it is likely these female counter tactics are designed to confuse paternity and reduce selection for aggressive male mating tactics including infanticide. It is also likely that a high degree of female mate choice has resulted in a low level of male-male physical conflict, and selection for males that invest time and energy in developing amicable relationships with females (East and Hofer, 2001). Although female spotted hyenas clearly prefer tolerant males, female mate choice is not biased towards a few male clan members. Therefore, genetic compatibility may also be a component of mate choice (East et al., 2003).

2.2 The commuting system

At the heart of spotted hyena social life in the Serengeti National Park is the commuting system (East and Hofer, 2002), which enables all members of a clan to minimise escalated conflict over access to food resources within the group territory. The Serengeti ecosystem includes grassland and woodland, plains, kopjes, and marshes, and the herbivore biomass is dominated by migratory species, chiefly wildebeest (*Connochaetes taurinus*), Thomson's gazelles (*Gazella thomsoni*) and zebras (*Equus burchelli*), which are the primary prey of Serengeti spotted hyenas. However, due to the movements of migratory herbivores, prey abundance within the clan territory varies throughout the year, leading to periods of high-, mid, and low prey abundance. High prey abundance (mean of 238 amimals/km^2) within any given territory occurs only 22-30% of any year (Hofer and East, 1993a).

Unlike most carnivores, which rely on the resident prey throughout the year, Serengeti spotted hyenas feed predominantly on migratory herbivores. When large migratory herds are present, all clan members forage within the clan territory. However, as prey abundance declines, conflict between clan members over access to food increases (East and Hofer, 2002). During periods of mid- and low-prey abundance, conflict among clan members over access to food in the group territory can be reduced by individuals leaving the clan territory on short-term (6-8 days for non-lactating animals), long-distance (40-80 km) foraging trips to the nearest concentration of migratory herbivores. These commuting trips become more frequent as the density of prey abundance declines (Hofer and East, 1995). Subordinate individuals frequently commute when herbivore density within the clan territory is moderate, while females of higher social status only commute when conditions of low-prey abundance prevail, since top-ranking females always have priority access to resources in the territory and are not challenged by lower-ranking females.

Despite the energetic cost and physiological stress (Goymann et al. 2001b) associated with frequently long distance foraging trips, which result in individuals being absent from their home territory for several days, individuals may gain considerable nutritional benefit during their foraging excursion; an outcome that is only possible because of their flexible behavioural response to changes in food abundance. Furthermore, under

conditions of medium prey availability, females of medium and low rank can sometimes be more successful at finding food when commuting alone, compared to dominant females with more privileges that remain in the home territory. Therefore, the costs and benefits of social status may vary with food availability.

2.3 Dynamic relationships of dominance and submission in female spotted hyenas

Spotted hyenas are extremely social and interact with other members of the clan. The communal den inside a clan territory is an important social centre for the group and as a consequence, many different types of interactions can be observed in the general vicinity of the den. Interactions between individuals take place either in dyads or groups of more than two individuals. During one-to-one meetings, social status is usually established amongst the participants, in which one individual nearly always signals his or her acceptance of their subordinate social status by expressing submissive gestures. These interactions are normally used to construct the dominance hierarchy, which are based on submissive gestures independent of competition for resources.

Frank (1986b) however, used frequency of displacement at kills to determine social rank, presumably under the assumption that a dominant animal will always displace a subordinate one when the carcass is not big enough to allow all animals to feed simultaneously. The problem with Frank's method is a degree of circularity in the argument concerning the benefit of social status. Social status it is argued provides priority of access to food resources. However, by using access to food as a measure of dominance, Frank does not take into account that dominance may vary depending on the context. For example, in some species dominance alters in different contexts, often with males being generally dominant, but males submitting i.e. allowing their female partners to feed first when they have young. Therefore, what needs to be shown is whether animals are dominant away from food, and then to determine whether dominant animals gain priority access to feeding sites. Once an animal is satiated it is no longer necessary to assert dominance, thus, subordinate animals may easily be granted access to the carcass when dominant animals no longer wish to feed. The remaining subordinate individuals then need to sort out their feeding priorities with the remaining animals at the carcass.

Spotted hyenas have a ritualised greeting ceremony during which the subordinate participant erects her enlarged penile clitoris ("pseudo-penis"), presenting it for inspection by a dominant animal (East et al., 1993). In one kind of greeting ceremony, a subordinate individual seeks out a dominant animal to initiate a greeting, which is an active form of submission. Conversely, an individual may also try to force another to greet by standing over an animal that is lying down. After conflicts greetings may also be initiated either by dominants or subordinates (Hofer and East, 2000). An animal will usually initiate several greetings after being away from the communal den or when separated from other individuals for a long period of time. This appears to be important for reconfirming that they are part of the group and to re-establish their place in the hierarchy, since relationships may change while an animal is away. Greetings between males and females are rare and when they do happen it is usually between adult females and top ranking immigrant males. Finally, group interactions usually take the form of coalitions, which I will discuss in detail later on. Spotted hyenas are well adapted to work together in groups, which can be observed in a typical territorial encounter with a neighbouring clan, or when challenging female lions.

2.4 Siblicide

'The contractions deepen and the births begin. One hour apart, the two cubs emerge, their eyes open, incisors and canines fully developed. The exhausted mother licks her offspring. But within minutes the scene turns nasty as the first-born cub grips its twin over the shoulders and shakes it. The pair roll in a bitter embrace each with the skin of the other locked in its jaws' (Laurence Frank, 1994, p. 38)

In a review paper Frank et al. (1994) published a highly emotive account of his sightings of siblicide that had taken place in the Berkeley spotted hyena captive colony (also see Frank et al., 1991). Frank stated that he was surprised that he rarely saw a mother with twins, or mixed sex litters in wild populations of spotted hyenas in the Masai Mara National Reserve in Kenya. Thus, after witnessing siblicide in the captive colony he concluded that spotted hyenas are 'genetically programmed' to kill their siblings, as a by-product of selection for androgens. Also, he stated that a hyena mother intervenes in fights to tailor the sex ratio of her litter according to her own rank. Frank suggested that daughters that remain on a territory would compete with their mother,

while sons disperse when reaching adulthood and thus, don't compete with their mothers. Conversely, if there is little competition between females, for example, when they are few in numbers, mothers may switch to supporting daughters as to rebuild a maternal core. However, Frank did not consider the importance of mother-daughter relationships for the recruitment of valuable coalition partners that are critical for the maintenance of social rank. Instead, he argued that high-ranking mothers should benefit (in an evolutionary way) if they produce successful sons that end up being alpha males in other groups. Also, he did not know that females exercise a high degree of mate choice, thus even though on a behavioural level it may be assumed that top ranking males should sire most offspring in the group, in spotted-hyenas this is in fact not the case.

Following this highly controversial publication, other scientists took interest in studying this phenomenon in wild populations of spotted hyenas. Contrary to Frank et al. (1991), other studies point towards a facultative model of siblicide, which occurs only when there are insufficient resources to sustain two cubs (Smale et al., 1999; Golla et al., 1999; Wachter et al., 2002), which would result in siblicide being less common than previously supposed by the habitual siblicide theory. Contrary to the habitual model, siblicide in the Serengeti population conforms to predictions from avian models of facultative siblicide (Golla et al., 1999). These models predict that the dominant sibling will monopolise the available resources when food is provided at a low rate, since the resulting fitness benefits for the dominant sibling outweighs the costs of fighting with and causing the death of the subordinate sibling. However, if parents are able to supply sufficient food for both offspring, then it is expected that dominants will not displace subordinates because the fitness gained from monopolising food relative to sharing resources is low or non-existent (McNamara et al., 1994). In one litter (Hofer and East, 1997), aggression between siblings was observed on the day of birth, which involved pushing and biting. Cubs could grasp their sibling with their jaws, shaking the head violently, which resulted in physical damage. Sibling aggression led to the establishment of a dominance hierarchy between littermates, which influenced priority access to teats. However, physical injury was a very unlikely cause of death. Siblicide normally occurred within the first two months of life when a dominant cub prevented the subordinate sibling from suckling (Hofer and East, 1997; Golla et al., 1999). If a dominant cub consistently excluded it's sibling from suckling, then the rate of growth in

the subordinate cub would decrease significantly. Eventually, if the asymmetry in growth between siblings were to become extreme, then the subordinate sibling would die of starvation. The mean age at which siblicide occurred, was 86 ± 70.5 days (median age 68 days, n = 22, minimum age 12 days, maximum age 273 days; Hofer and East, 1997).

A later study on siblicide in Serengeti spotted hyenas suggests that siblicide is facultative, since rates of sibling aggression increased inversely with levels of maternal input (measured in terms of cub growth). Also, the rate of aggression was lower in those cubs belonging to higher-ranking females, who receive higher levels of maternal input, compared to cubs belonging to lower-ranking mothers, who receive less in terms of maternal input. Furthermore, Ngorongoro spotted hyenas (Ngorongoro Crater, Tanzania) live in a prey rich environment (176 animals/Km^2), unlike Serengeti spotted hyenas (3.3 animals/Km^2). As predicted by avian models of facultative siblicide, sibling aggression between Ngorongoro spotted hyenas was substantially lower compared to Serengeti spotted hyenas (Wachter et al., 2002). Also, there was no evidence of siblicide in the Crater, while facultative siblicide in the Serengeti is relatively common.

It has also been suggested from evidence on the sex ratios in Masai Mara siblings, that mothers pre-natally manipulate the sex of their cubs (Holekamp and Smale, 1995; Smale et al. 1999) to allow for local resource enhancement (LRE: see Gowaty and Lennartz, 1985). In this scenario, LRE would predict that when the level of competition is high in the clan territory, mothers should produce more males, which disperse and thus reduce competition. However, when competition is low, mothers should give birth to more females. If it were the case that females adjust the secondary sex ratio of their offspring, then we would expect to find the same bias in siblings born in other clans. However, in the Ngorongoro Crater, sex ratios conformed to binomial expectations, contrary to the predictions of the LRE hypothesis (Wachter et al., 2002). Therefore, it is more likely that spotted hyena cubs adjust their level of within-litter sibling aggression in an adaptive manner, according to the predictions made by avian models of facultative siblicide (Wachter et al., 2002)

In conclusion, these findings do not support the idea that siblicide in hyenas is independent of resources, with mothers capitalising on siblicide to tailor the sex ratio

for their own benefit (Frank, 1994). Instead, spotted hyena cubs adjust levels of aggression in response to the amount of food they receive, which may as a consequence lead to transient changes in the sex ratios depending on the degree of competition between siblings (Hofer and East, 1997; Wachter et al., 2002). In Ngorongoro spotted hyenas, where competition for resources is less severe than in the Serengeti, there is no bias in the sex compositions of litters. However, in Serengeti spotted hyenas, which are exposed to fluctuating levels of resources in the clan territory, male-female litters are more common than male-male litters followed by female-female litters (Hofer and East, 1997). It has been hypothesised that changes in the sex-ratio, relative to resource abundance may reduce competition between females over food, because females, unlike males, stay in their natal clan and are dependent on the resources in the clan territory (Golla et al., 1999).

2.5 Patterns of associations in relation to the social status of animals

In this study I investigated whether female social rank influences choice of coalition partners. A model of primate affiliative behaviour assumes that the benefits derived from social relationships with different individuals are not equal (Seyfarth, 1977). The model (Seyfarth, 1977) predicts that associations with animals of adjacent rank were more valuable than with animals of lower rank. Therefore, it was concluded that animals should compete for grooming chances with preferred partners. The model also predicts that grooming can be exchanged for coalitionary support and that associations depend not only on rank, but also with the level of access to, or availability of, possible partners of different status (Silk et al., 1999). The general applicability of the model, in particular the prediction that individuals will compete to associate with animals of high social status, has been debated in the literature (Schino, 2001). Schino used meta-analytical techniques to test the expectations of the Seyfarth model in 27 primate species. He used published data that reported a matrix of grooming exchanged among adult females. On the whole, Shino's results support the assumptions of Seyfarth's model: Attraction to high social status; attraction to kin; and competition for higher-ranking grooming partners. However, Shino did not find a positive association between animals that groom each other and those that support each other in aggressive interactions. Shino emphasised that his analysis only compared the amount of grooming received by animals of different social status, but lacked data on forms of reciprocation

such as tolerance and coalitionary support. Also, 22 out of the 27 groups used in Schino's study were cercopithecine primates, which may have biased the results, since New World monkeys tend to show more variety in their grooming patterns compared to old world monkeys. For example, in captive brown capuchin monkeys (*Cebus apella*), females at the top of the social hierarchy initiate more grooming bouts than are initiated by others with them (Parr, 1997).

This variability in the distribution of grooming in different groups can be explained because grooming performs different functions in different contexts. For example, it is possible that capuchins reciprocally exchange a wide range of "currencies," from allonursing to agonistic alliances, and from food sharing to coordinated hunting. Thus, the tendency in female capuchins to groom lower ranking partners may function to encourage low-ranking females to lend support or voluntarily share food with high-ranking females (de Waal 1997a).

The more recent paradigm of biological markets (Noë and Hammerstein, 1994) has been used to explain the variety of grooming patterns and associations between animals because the value of grooming is dependent on the benefits received. Some hunter-gatherer societies for instance, use meat gifts to secure political allies (Patton 2004). Thus, the theory proposes that grooming is exchanged for other commodities such as coalitionary support, food, tolerance from dominants, or protection against predators. For example, it has been suggested that associations between different species evolved as a response to increased predation pressure (Noë and Bshary, 1997).

The biological markets paradigm assumes that different types of grooming relationships fulfil different purposes such as social support against group members, access to food, tolerance etc. However, one assumption of the biological markets framework is that grooming is unimpeded by restrictions on access to partners (Henzi et al., 2003). This is not the case in spotted hyenas, who predominantly greet more dominant individuals, and access to dominant females by subordinate females is dependent on the dominance status of those animals present in the clan territory. A long-term study on greeting in Serengeti spotted hyenas (East et al., 1993) largely supports the predictions of Seyfarth's model for grooming in primates, in that individuals adjacent in rank greet more frequently compared to those that are not similar in rank. However, participants in

spotted hyena greeting ceremonies deviate from the expectations of Seyfarth's primate model, because mid-ranking females regularly greet high-ranking females. This may be explained by the fission-fusion society characteristic of spotted hyenas in the Serengeti (where females regularly leave the clan territory on commuting trips), in which access to high-ranking females by mid-ranking females is not always curtailed by those above them in the hierarchy (East et al., 1993). Thus, access to greeting partners depends on the absence or presence of socially dominant females.

In conclusion, models of social greeting and grooming patterns need to consider the variety of social and ecological circumstances that are likely to influence associations amongst animals. Animals demonstrate a variety of greeting patterns that seem to depend on the specific types of relationships that are valuable to individuals. Thus, greeting and grooming patterns are valuable interactions in the social environment and animals that distribute their interactions in a fitting way, benefit the most from them and gain an evolutionary advantage.

2.6 Coalitions and how they mediate changes in social status

Female coalitions are common in many animal groups including primates (Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997; Isbell and Young, 2002), and social carnivores such as the white-nosed coatis (*Nasua narica*) (Gompper et al., 1997) and spotted hyenas (East and Hofer, 2002). In spotted hyenas coalitions are important because individuals can reinforce their social status and, as a consequence, this stabilises the dominance hierarchy, though very occasionally coalitions can result in rank reversals. Social status is very important for a female hyena as this directly influences access to food, which in turn determines her health status and the probability of her cub surviving (because the quantity of food consumed will determine how much milk a female can produce and how much solid food her young will receive when it is old enough to eat solid food -- as it obtains a social status in feeding situations immediately below the mother's status). Females need to be tactful when interacting in a coalition. For example, an animal that joins another to form a coalition against a "victim" must judge that it has a stronger social bond to the animal it supports than the

"victim" has to this individual. If this is not the case, then the supporter may be attacked by the victim (without it receiving any reciprocal support from the animal it sought to support), or the animal it sought to support might reject the gesture, by exerting dominance over the animal and forcing it away (in which case the victim may take the chance to also exert dominance).

In Serengeti spotted hyenas, the strength of a coalition is likely to depend on which coalition partners are regularly present in the clan territory, since the more often animals interact with their coalition partners, the stronger the coalition is likely to be. Furthermore the absence of normal coalition partners may lead to changes in coalition partners with an associated increase in the strength of bonds with the new partners. During periods of low prey abundance, females with dependent cubs at the communal den inside the clan territory have to commute more frequently compared to non-reproducing females because they need to return to nurse their cubs (Hofer and East, 1993b). As a consequence, relationships among females may alter, since individuals commute at least 40km away from the clan territory when food is low and may be apart from other clan members for up to several months. Therefore, females become unsure as to which females are still alive and therefore the structure of the current hierarchy may become less stable.

Once relationships of dominance and submission are established, social relationships are relatively stable and levels of aggression rarely escalate (East and Hofer, 2002). If individual interactions in the dominance hierarchy can, as a consequence, reinforce the stability and linearity of the hierarchy then I would expect coalitions to be formed between females of similar social rank (i.e. adjacent in the hierarchy), who resist take-over by potential revolutionary alliances. However, coalitions can also be used to challenge existing social structures, and this usually occurs when a subordinate coalition recruits a new member (e.g. when a daughter reaches adulthood) or when an individual in a dominant coalition dies or is absent for an extended period when commuting. If a subordinate animal joins a coalition it can increase in social rank if that coalition wins, equally, if a high-ranking coalition loses, then the whole coalition may drop in rank. When coalitions gain or lose strength then periods of social instability and unrest result and the hierarchy becomes non-linear. For example, if the leader of the clan dies or many individuals are away for long periods on commuting trips, the female hierarchy

can become temporarily non-linear (M.L. East, personal communication). Under these circumstances the loss or gain of a coalition partner can lead to changes in social rank. Thus, coalitions may stabilise or destabilise social relationships (de Waal, 1997b). During periods of instability, joining a coalition to challenge the status quo is risky, since an individual may become badly injured or drop in social rank if the challenge fails. Conversely, members of a winning coalition become socially dominant over the losing coalition. Choosing not to fight reduces the risk of becoming injured in a damaging conflict. However, choosing not to be involved can still cause their social rank to change as a result of interactions occurring between other individuals.

Fitness costs associated with a decline in social status depend on the amount of resources lost as a result of the decline. For example, when resources are abundant in the clan territory, social rank does not affect the nutritional status of individuals because there is enough food to feed all clan members. However, when resources become less abundant (i.e. medium prey abundance) then a high-ranking female that drops in social status will have to commute to find food, whereas previously she could monopolise low-cost foraging opportunities within the clan territory (East and Hofer, 2002). In this scenario, the former high-ranking female may be exposed to a greater loss in her elevated nutritional state from an erosion of her priority access to food, compared to a lower-ranking female that also dropped equally in rank, since the latter had very little feeding rights even prior to her decline in rank. However, this also depends on how efficient the former higher-ranking female is at finding food outside the clan territory, and whether she has cubs to feed, since maternal effort increases considerably when mothers commute, often resulting in a reduction in the growth rates of their offspring (Hofer and East, 1993c).

Do the benefits and costs of being a high-ranking or low-ranking female vary depending on the context? Mid- and low-ranking females may have acquired superior skills at finding prey outside the clan territory, since they commute more frequently throughout the year compared to high-ranking females. On the other hand, higher-ranking females may suffer less cost compared to lower-ranking females when food gets extremely low, due to their higher nutritional status. Therefore, the relative costs for high-ranking vs. low-ranking females may be context-dependent. However, before drawing any conclusions, these relative costs need to be quantified.

A previous study on coalition formations in a captive group of prepubertal spotted hyenas (Zabel et al., 1992) showed that higher-ranking individuals were more likely to join an ongoing attack compared to lower ranking ones. Also, lower-ranking individuals were targeted more frequently compared to higher-ranking animals. Comparable studies on wild populations are more desirable since they offer ecological validity to results, which is not possible in captive colonies. Animals in captive situations frequently elicit different types of behaviours and are often more aggressive (Hediger, 1964; Mech, 1999; Goymann et al., 2001a). Second, Zabel's population consisted of prepubertal males and females, while in wild populations males typically leave their natal clan when they reach maturity, and adult females have established social relationships. Male dispersal may have important consequences for relationships of dominance and submission in the female social hierarchy, which might be obscured in captive populations.

3. Aims and objectives of my study on Serengeti spotted hyenas

In this study we investigated whether associations in female spotted hyena coalitions follow a pattern similar to those predicted by Seyfarth's (1977) model of primate affiliative behaviour. Social bonds change in relation to social rank, and the position acquired within the social network influences individual fitness (Holekamp et al. 1996; Hofer and East, 2003). Coalitions resulting from interactions between adjacent individuals may, as a consequence, stabilise the female dominance hierarchy. Similar-ranking animals usually have similar objectives, which is to maintain their social position and move up the hierarchy when an opportunity arises. High-ranking females may engage more often in coalitions compared to low-ranking females because the former may suffer more costs, relative to the latter, following a decline in social status (this depends on how much each female drops in rank and the relative amount of resources lost). However, high-ranking female coalitions are very occasionally overthrown by a lower-ranking coalition during periods of unrest. Therefore, due to the fission-fusion society of spotted hyenas the social hierarchy is liable to become less stable during times when most females are away for several weeks on commuting trips. Therefore, I also used unpublished data from Marion East, recorded during periods of instability.

If coalitions in spotted hyenas do affect an individual's fitness by decreasing, maintaining or increasing social rank, then I would expect coalition support to be stronger and more frequent between females of adjacent rank in the hierarchy in a manner which is consistent with the predictions of Seyfarth's model (Seyfarth, 1977). This model predicts that low-ranking females are attracted to high-ranking females, because the latter can provide superior support during agonistic encounters. As a consequence it is expected that females compete over access to high-ranking females. This competition prevents low-ranking females from accessing top-ranking animals, due to competition with mid-ranking females. This results in females tending to associate with those next to them in the hierarchy and, as a consequence of this, a linear hierarchy is maintained. Thus, I predict that the ranks of coalition partners, i.e. the initiator and supporters, should be similar. Also, I predict that initiators and supporters target animals that are adjacent but slightly lower in rank, relative to their own position in the hierarchy, since this is perhaps a way in which higher-ranking females can communicate their relative dominance and availability of coalition partners to potential rivals. Finally, I expect that coalitions are most common in top-ranking animals because these animals have preferential access to resources in the clan territory. Therefore, top-ranking animals are expected to invest in social bonds that help maintain their position and secure coalition partners, and are likely to engage more frequently in agonistic encounters compared to lower-ranking females.

Fights can be costly to females in two different ways. First, fighting may incur physical damage to females such as wounds resulting from bites, which may become infected and disable the injured individual. For example, it is common to see spotted hyenas with torn ears, resulting from fights with other clan members (Marion East, personal communication), which emphasises the degree of damage individuals can inflict upon each other. Second, fighting can also be costly when a female coalition loses a conflict against another female coalition. This results in the losing coalition dropping in social rank, which decreases their absolute feeding rights in the clan territory. Therefore, it is expected that females will fight for their position in the dominance hierarchy when the fitness costs resulting from a drop in social rank exceed the costs of risking injury.

Finally, I also describe some interesting aspects of hyena social life from my own observations and personal communication with Marion East. Spotted hyenas demonstrate a rich variety of interesting behaviours, which I will describe and discuss from an evolutionary perspective.

3.1 Methods

3.1.1 Study site, context and background

I studied spotted hyenas in the Seronera valley in the centre of the Serengeti National Park in northwestern Tanzania, East Africa in association with a long-term study led by Marion East and Heribert Hofer (Institute for Zoo and Wildlife Research, Berlin) . Two other long-term studies on spotted hyenas exist in the Serengeti Ecosystem; one in the Ngorongoro Crater conservation area (south-east Serengeti, see Höner et al. 2005) and the Masai Mara Reserve (in Kenya, see Holekamp et al. 1996).

Three different clans, the Isiaka's, Mambas and Pools, have been studied extensively in the Seronera valley, Serengeti over the past 20 years (Hofer and East, 1993a,b; East and Hofer, 2002). All clan members are individually known and the social hierarchies for each of the clans is known and constantly updated. Genetic analyses using microsatellite data are used to determine which individuals are related, and which males sire cubs (East et al., 2003). Access to the clans is possible only in a vehicle because of the presence of potentially dangerous animals. During my study period, data on the Pools clan were limited, since they moved away from their previous communal den and it was not possible to relocate the clan. Therefore, I did not use this limited data for my study.

Since I arrived during the wet season, the grass was approximately 1 metre high. Although it was dry during my study period from February to March, access to the communal den areas was quite challenging due to the high vegetation, which also made it more difficult to identify individuals. However, with almost 20 years of experience in the field, Marion East, who accompanied and supervised all my observation periods, was able to overcome these problems. All study animals had names and identification numbers. Numbers were used in the analyses of data, while in the field individuals are always referred to by their names. At night, observations were made using a torch from

a stationary vehicle parked about 15 metres from the den. The animals were habituated to observation using torchlight from birth or early years and we detected no discernible change in their behaviour as a result.

3.1.2 Observation periods

Most observations took place at the communal dens of three clans where cubs are raised together for at least 12 months after birth (Hofer and East, 1995). Data were collected over five weeks from February the 2nd to March the 10th 2004. Daily observations on interactions at communal dens were made at dawn and dusk (between 0600-0900 and 1600-2100). Since animals are constantly returning to and leaving the communal den there were usually about 15 individuals present at the communal den at any one time. Observation periods were set at times when most animals were likely to be present at the den (East and Hofer 1991a,b) to increase the chance of observing coalitions and other interesting interactions. Evening observations until 9pm were most useful since all-night watches have revealed that most individuals arrive at the communal den before 9pm. Morning observations before 9am were also useful, but after this time most animals usually go to sleep under trees, due to the mid-day heat, and are not active until around 4pm when it starts to cool.

This study was conducted during the wet season when herds are expected to be in the South of the Serengeti National Park. However, since it did not rain for most of my study period, migratory herds were present for about one week in the study clan territories, but moved out again when the rains started. This was fortunate because it enabled me to record hyena behaviour and their social interactions in both prey rich and prey poor conditions.

3.1.3 Prey abundance

During their annual migration, the large herds of wildebeest, Thomson's gazelles and zebras move twice along a rainfall gradient. At the start of the rains in December, the herds leave their dry season woodland refuges in the north and west of the ecosystem and move to the highly nutritious short-grass plains in the southeast where they give birth. The herds leave the plains at the end of the rains in May and move to the dry

season areas where they remain until November-December (Hofer and East, 1993a). Thus, during the wet season, herds are south of the Seronera valley, while in the dry season they range north of the valley. As a consequence of these movements, herds are never present in the region where our study clan territories were situated for more than a few months (East and Hofer, 2002), since Seronera is in the centre of the Serengeti.

3.1.4 Social Status

Females have matrilineal relationships, in which offspring usually acquire a social rank just below their mother. However, this does depend strongly on the support by mothers (Hofer and East, 2003). Female social status was determined during dyadic interactions whereby the individual displaying submissive gestures was categorised as subordinate. The data was used to construct the female dominance hierarchy following East and Hofer (1991a,b). According to this method, social rank is determined chiefly from submissive acts and occasionally from aggressive acts (see Table 1) in individual interactions recorded *ad libitum* (Altmann, 1974) and during focal observations of individuals. Individuals with ranks within the top, middle, and lower third of the total range of values are classified as high-, mid-, or low-ranked (see Goymann et al. 2001b). Social status is continuously assessed and defined during periods when there is no change in the hierarchy. A new period starts when an individual dies, or during times of instability, in which the social ranks of individuals can change on a daily basis. Periods of social instability can be followed by several years of social stability. During my period of study the hierarchy was stable, which stretched over a year.

3.1.5 Clan size and the number of females present during watches

During my study the Isiaka and Mamba clans had a similar group size of approximately 36 females. The number of females present during my study in the Isiaka and Mamba clans was also similar (Isiaka: 27, Mamba: 24). This is important when comparing data on interactions in different clans, since the number of females present in the clan territory during watches may affect choice of coalition partners and the frequency of coalition formations. Finally, during my study period the ranks of females that were present at the den were evenly distributed in both the Mamba and Isiaka clan.

Therefore, I was able to observe and record coalitions in females of high-, mid- and low rank.

3.1.6 Identification of individuals

I applied the same method used by Golla et al. (1999) for determining adult identity, which were identified by their distinctive spot patterns that remain throughout an individual's life time, despite fading slightly with age. Other recognisable features include ear damage or other kind of injury or markings (Frank, 1986a). Marion East helped to identify individuals, since this is a skill that takes several months to master properly.

3.1.7 General observations and recording of behaviour

The ad libitum (Altmann, 1974) method was used to collect data on differences between male and female behaviour, mate choice, conflict and play behaviour. Here, the aim was to gain a personal understanding of spotted hyena social life, which is why I spent time simply interpreting the purpose of the behaviours and interactions of individuals around me. I also include published and unpublished data from Marion East, since she was able to interpret what I was seeing based on her detailed knowledge.

3.1.8 Types of coalitions

Coalitions are formed when one individual recognises that another individual requires assistance (e.g. when one female whoops to alert other females that a lion is near the den, in which case other females are recruited to help drive the lion away). These coalitions are usually large because all clan members need to pull together to scare away potential danger. However, the coalitions I report are usually composed of 2-4 individuals and are strictly coalitions formed by clan members against other clan members, for which there are three main types: a) Coalitions when there is no clear "target", rather females are cementing their social bonds. They do this by walking together parallel; b) coalitions that are formed when one individual initiates an interaction with a second individual and on observing this a third individual either joins the interaction by forming a coalition with the initiator to exert social dominance over

the second, or; c) the third individual joins the interaction to support the target against the initiator.

The most typical coalition involves a female approaching another individual in an assertive manner, which usually involves standing over or/and pushing against the animal. The initiator is joined by at least one other animal, which also approaches the target assertively and may occasionally escalate aggression. I did not observe any coalitions in my study period, in which a third individual supports the "target" against the initiator. Most coalitions, in which only one individual is approached, are harmless and result in the challenged animal submitting. Display coalitions are also frequent in which two or more individuals walk side by side (parallel walking) with their tails up. In this situation no individual is challenged. Sometimes females form coalitions with top-ranking males, however, I only used data on female coalitions to analyse choice of coalition partners and targets, since immigrant males are all subordinate to females and do not fit into the female social hierarchy. Sometimes we were only able to spot a coalition once they were already formed, particularly when it was dark in which case it was not possible to know which animal initiated the coalition. In these cases, I recorded all coalition 'aggressors' as supporters. This did not pose a problem since I obtained sufficient data on the rank of initiators of coalitions in other interactions.

3.1.9 Behavioural Sampling

All coalitions amongst females were recorded from the 5th of February 2005 to the 9th of March 2005 (26 days of data collection, 100 interactions observed) during the daily observation periods between 0600-0900 and 1600-2100, because this is when the animals are most active. Submissive and assertive behaviours were recorded (see Table 1), as well as the identities and social rank of the initiator, target and supporters involved in each interaction.

Table 1. Description of aggressive and submissive behaviours

Submissive behaviour	Aggressive behaviour
Ears back	Lunge
Tail between legs	Bite
Head upside down	Approach with tail up
Head bobbing	Push
Teeth bared	Stand over
Retreat	Tail up
Side step	Stand over pushing broad side
Erect clitoris	Wrap neck
Mouth wrestle	Chase
	Walk tail horizontal
	Walk parallel with tail up
	Preventing cubs from suckling

3.1.10 Statistical Analyses

The majority of data used for determining the social rank of animals were collected at communal dens during observation periods. Marion East determined the social rank of individuals prior to my study period, and I was able to use this data for my study. The social rank of adult clan members was based on an interaction matrix using aggressive actions and submissive reactions (see Table 1) in dyadic interactions recorded *ad libitum* (see East and Hofer, 1991a; East et al., 1993). I was able to test for correlations between the ranks of coalition members: initiators, supporters, and targets using Spearman rank correlations. The Spearman rank test is suitable to assess whether a factor is correlated with a rank variable. In this study I used the terms 'initiator', 'target', and 'supporters' to describe individuals that were involved in coalition interactions. Supporters form a coalition by helping a female (initiator) that has challenged another individual (target). I investigated whether there existed relationships between the 1: target rank and initiator rank; 2: single supporters ranks and the initiator rank; 3: median support rank and the initiator rank; 4: median coalition rank and target

rank; and 5: number of coalitions a target, initiator or supporter was involved in, and their social rank. In a typical coalition there were usually one or two supporters. There are two possible ways for representing the support rank. When there was more than one supporter in a coalition, I separated the coalition data into dyads each consisting of an initiator and a single supporter (i.e. initiator-supporter 1; initiator-supporter 2; initiator-supporter 3; and initiator-supporter 4). Or, one can take the median value of supporters in a coalition. I used both methods to test whether the alternatives were consistent. Finally I also analysed statistically whether 1) the ranks of initiators were higher than the ranks of their targets, 2) supporters were higher-ranking than targets, and 3) initiators and supporters were equally likely to be the more dominant animal.

I divided Figures 1-3 into four areas by drawing two perpendicular reference lines on the x and y axes at the median rank of 18.5. In Figure 1 for instance the top left area shows interactions that occur between mid-high ranking targets and low-mid ranking initiators. The top-right area shows those interactions that occur between mid-high ranking targets and mid-high ranking initiators. Data points (in Figures 1-3) do not represent the actual number of interactions (*N* value), since a number of interactions occurred more than once. For example, a female with the social rank of 17 initiated 2 separate coalitions against a female ranked 24 in the hierarchy.

Finally, since this was a short-term study, my data set alone was not sufficient for quantitative analyses. Therefore, I included data from previous field seasons (Marion East, unpublished data), which were collected using the same methods.

3.2 Results

3.2.1 Relationship between the target rank and initiator rank

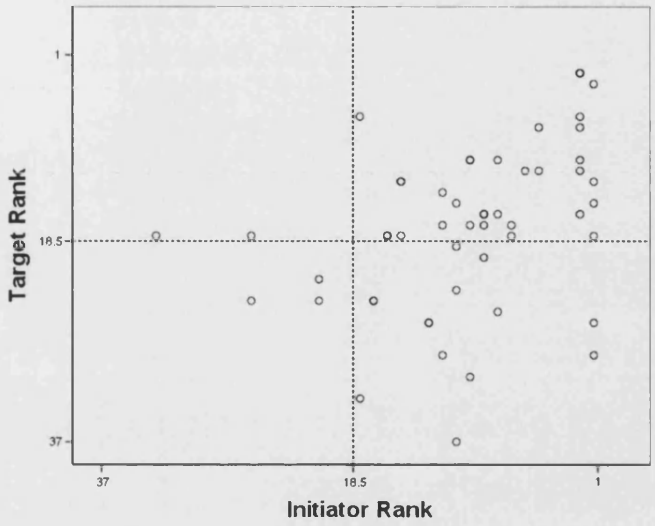

Fig 1. The relationship between the social rank of target individuals and social rank of initiators (r_s = 0.426, P = 0.002, N = 52). Social status is ranked in order from 1 (highest) to 37 (lowest); median rank is 18.5.

3.2.2 Relationship between the support rank and the initiator rank

The relationship between the single support ranks and the initiator rank (r_s = 0.321, P = 0.002, N = 90; Figure 2a) is consistent with the results obtained from the relationship between median support rank and initiator rank (r_s = 0.342, P = 0.004, N = 69; Figure 2.b).

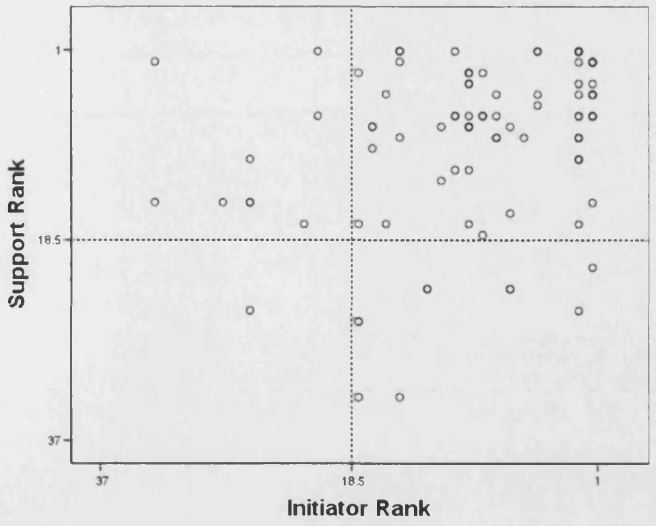

Fig 2.a. The relationship between the social rank of supporters and initiators using dyadic interactions each with an initiator and one of the supporters ($r_s = 0.321$, $P = 0.002$, $N = 90$). Social status is ranked in order from 1 (highest) to 37 (lowest); median rank is 18.5.

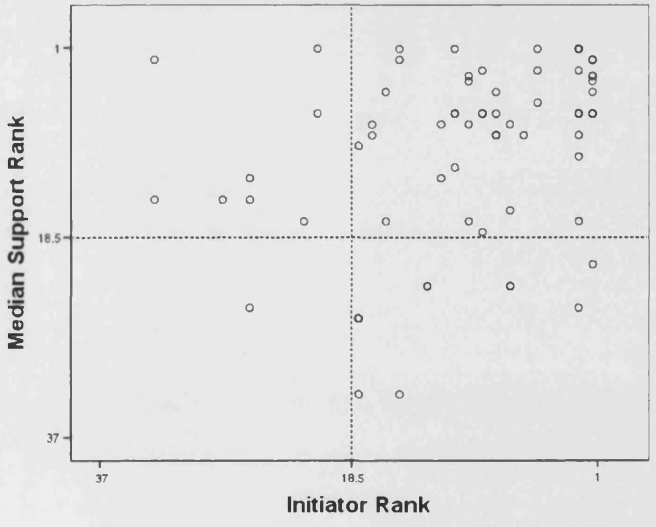

Fig 2.b. The relationship between the median social rank of supporting members of a coalition and the social rank of the animal that initiated the coalition ($r_s = 0.342$, $P = 0.004$, $N = 69$). Social status is ranked in order from 1 (highest) to 37 (lowest); median rank is 18.5.

3.2.3 Relationship between the median coalition rank and the target rank

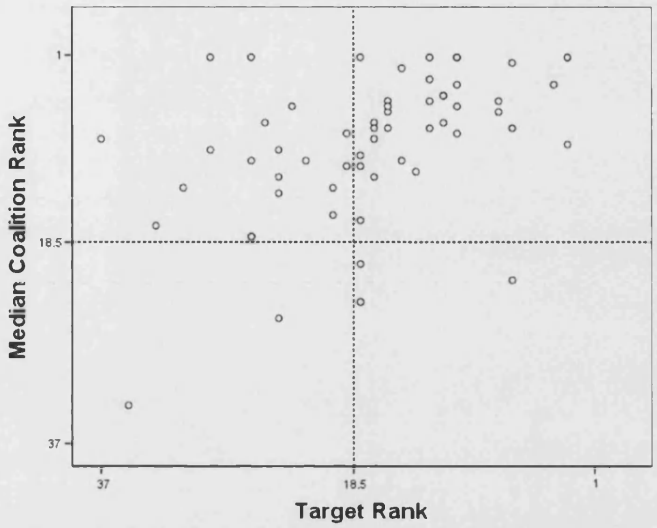

Fig 3. The relationship between the median rank of individual members of a coalition and the target rank (r_s = 0.516, P = 0.001, N = 60). Social status is ranked in order from 1 (highest) to 37 (lowest); median rank is 18.5.

3.2.4 Relationship between the number of times a female was involved in a coalition and female social rank

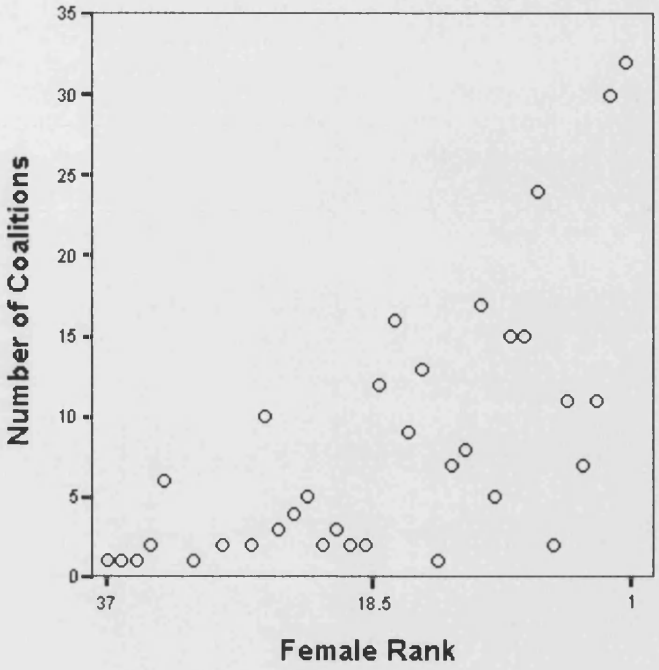

Fig 4. The relationship between the number of times a female was part of a coalition and female rank (r_s = 0.702, P = 0.001, N = 34). Social status is ranked in order from 1 (highest) to 37 (lowest); median rank is 18.5.

3.2.5 Are initiators higher-ranking than their targets? Are supporters higher-ranking than targets? Are supporters and initiators equally likely to be dominant?

In most interactions, initiators were higher in rank compared to their targets (P = 0.001, Mean = 0.8846, Std. Deviation = 0.32260, N = 52). Also, supporters were higher-ranking than the targets of a coalition (P = 0.001, Mean = 0.9012, Std. Deviation = 0.30021, N = 81). However, there was no significant difference in the probability of supporters or initiators being the dominant animal (P = 1.000, Mean = 0.500, Std. Deviation = 0.50287, N = 88).

4. Interpretation of my results and discussion of my qualitative observations

4.1 Summary and discussion of my findings

Ecological conditions, such as varying and unpredictable resource abundance, often favour the formation of social groups and communal territory defence. Similar to many cercopithecine primates (see Silk et al., 2004), Serengeti female spotted hyenas are characteristic of female philopatry, linear dominance hierarchies, and the acquisition of maternal rank, which together are thought to promote the formation of coalitions and alliances. The results of my study on coalition formations in female spotted hyenas suggest that female coalitions result in the stability of the existing female dominance hierarchy as a consequence of individual behaviours and associations. First, the initiator and target ranks were correlated (Figure 1), and, in most interactions, the initiator and supporters were more likely to be higher in social rank than their target. Second, the supporter ranks were also significantly correlated with those of the initiator (Figure 2.a and b). However, there was no difference in the probability of 1) the initiator rank being higher than the supporter rank and 2) the supporter rank being higher than the initiator rank. There was a significant relationship when comparing the median coalition rank with the rank of their targets (Figure 3). However, although initiators usually target adjacent females, there were also a number of interactions in which they challenged mid- or even low-ranking females (Figures 1 and 3). As expected, high-ranking females were observed more often in coalitions compared to lower-ranking females (see Figure 4).

A similar pattern exists in the greeting ceremonies of spotted hyenas, in which females of adjacent rank exchange affiliative gestures more frequently compared to non-adjacent females. However, this depends on which females are present at the communal den, since mid-ranking females can access high-ranking females when the intermediaries are absent from the communal den (East et al., 1993). Although greeting ceremonies may help secure valuable coalition partners that maintain the status quo, the same coalitions can also pose a threat to the status quo. For example, during periods of instability (i.e. when food is extremely low and most females are away from the clan territory for several days or weeks), associations are less rigid and unpredictable due to the absence of higher-ranking females, thus, relationships become less rank-related and

associations less predictable. Under these circumstances an individual's social status can shift dramatically in either direction depending on which other individuals are present, and the size of the coalitions competing for social rank (Marion East, unpublished data; also see Hofer and East, 2003).

Why are initiators generally higher-ranking than their targets, and why are coalitions more frequent amongst higher-ranking females? Social rank in female spotted hyenas determines annual commuting effort: Medium- and low-ranking lactating females travel a minimum average distance of 2900-3700 km annually, whereas high-ranking mothers only travel approximately half this distance (see East and Hofer, 2002). Therefore, high-ranking females suffer less cost in terms of commuting effort compared to mid-and low-ranking females. As a consequence, the reproductive success of higher-ranking females is higher compared to lower-ranking females, and their offspring are more likely to reproduce at a younger age with shorter inter-birth intervals (see East and Hofer, 2002). Therefore, since priority access to resources in the clan territory decreases with social rank, it is expected that high-ranking females will be more likely to invest in relationships and coalitions that help them to maintain their social rank and hence feeding rights in the clan territory, compared to low-ranking females. Also, lower-ranking individuals in coalitions rarely challenge a high-ranking animal, which reinforces the status quo.

The results of my study revealed that initiators were usually higher-ranking than their targets, and higher-ranking females were more likely to be involved in coalitions compared to lower-ranking females. Thus, the formation of coalitions in spotted hyenas appears to be largely dependent on individual rank. However, other factors may also influence whether animals participate in coalitions or not. First, 'personality' differences between individuals may influence whether they take part in coalitions. For example, some high-ranking females never take part in coalitions or conflicts (Marion East, personal communication). Second, Drea et al. (1996) proposed that play behaviour in infants is important for cementing their relationships. During my study period I observed adults and sub-adults engaging in play. However, it is unknown whether these interactions are related to coalitionary support. Also, future research questions should address whether kin attraction, greeting or previous coalitionary support correlates with the likelihood of future partnerships in coalitions.

East et al. (1993) found that both relatedness and social rank influence the pattern of social interactions in Serengeti spotted hyena clans. Associations with kin (Dunbar, 1980) and high-ranking females are considered to provide females with the highest benefits. If kin was the prime factor influencing female relationships, then it is expected that the proportion of kin greetings should be similar for high-ranking and low-ranking matrilines. However, if both rank and relatedness are predictors of female associations, then it is predicted that there should be a higher proportion of greetings amongst high-ranking matrilines compared to low-ranking matrilines. In spotted hyenas the latter appears to be the case, since offspring belonging to dominant mothers greeted their mothers more frequently than offspring belonging to lower-ranking mothers (East et al., 1993). These results are consistent with another study on spotted hyenas in the Masai Mara, in which social rank and kinship influenced association patterns in adult spotted hyenas (Holekamp et al., 1997). Finally, another study on spotted hyenas has shown that cubs mainly associate with littermates in coalitionary attacks against unrelated individuals (Smale et al., 1995).

In summary, my results on the pattern of female coalitions largely support the predictions of Seyfarth's models (1977) derived from associations in cercopithecine primates, which exhibit similar matrilineal rank-related relationships to spotted hyenas. However, my results do also show some exceptions to this rule, which may be related to the unpublished data from Marion East during periods of instability, which I included in my analyses. One weakness of my study is the fact that I did not record which individuals were present at the den during my behavioural observations. Therefore, my results may have been confounded by the fact that higher-ranking females tend to be present at the communal den more than lower-ranking females. Ideally, this study should have controlled for opportunity (i.e. which individuals were available to participate in coalitions) and potential threat (e.g. a coalition may overthrow a dominant animal if the coalition supporters of the dominant animal are not present at the communal den).

The arguments I have presented so far are likely to account for many of the behavioural patterns in individuals outlined in this Chapter. However, the social life of spotted hyenas is extremely complex, and there are many aspects of their social life that require

further explanation and appreciation. In particular, I am interested in how the commuting system, unique to Serengeti spotted hyenas, evolved. And why, despite the costs of leaving a group, do lower-ranking females accept a less 'ideal' situation? Are they really only doing the 'best of a bad job strategy'? Or, is there more to submission/receptivity than we think?

To address this question, I will dedicate the rest of this Chapter to my personal observations, interpretations and discussions with Marion East on other aspects of spotted hyena social life that is often not found in the scientific literature, partly because they are difficult to interpret and analyse quantitatively. This includes my own observations in the field, in which I described my observations of unusual and interesting behaviours. I also noted my interpretations of the behaviours and behavioural interactions I was observing at the time. To complement my own observations and interpretations, Marion East also shared her interpretations with me based on her previous experiences, published and unpublished data. When using unpublished data from Marion East, I referenced these discussions as: Marion East, personal communication.

I believe it is important to include my observations and interpretations in this Chapter because it allows me to identify possible biases in the animal behaviour literature or even inconsistencies in our logic and knowledge of these fascinating animals.

4.2 The communication of assertive and receptive behaviours

For the sake of convenience, I have adopted the conventional term: dominance hierarchy when describing the social structure of spotted hyenas. Nevertheless, this term may misrepresent the system, since established long-term dominance, not the type of dominance associated with winning a fight, is only possible if other individuals are willing to submit. Aggression, in the absence of receptivity could not create nor maintain the structure of the linear hierarchy in female spotted hyenas. For example, if an animal behaves aggressively towards either one or more individuals, then they can respond in a variety of ways, either by fighting back, submitting, ignoring etc. If aggression is countered by aggression then the result is escalated conflict. However, the possibility of forming cooperative relationships only becomes attainable if aggression is

countered non-antagonistically, for instance by actively submitting or by providing support. Thus, in spotted hyenas relationships of dominance and submission (e.g. in coalitions and greeting ceremonies) usually follow a ritualised pattern, rather than overt aggression, since the target submits before aggression is allowed to escalate.

However, these relationships do not always follow such a predictable pattern. For example, on one occasion I observed two individuals (one adult and one sub-adult) playing with a cub. It was obvious that the sub-adult female was being aggressive towards the other adult female, perhaps trying to impose her dominance (her mother was a very high-ranking female). Interestingly, the adult female appeared to be oblivious to the aggression directed to her from the sub-adult female and instead continued to play with the cub. Of course we cannot judge whether her behaviour was a deliberate strategy to avoid submitting and diffuse the aggression. Nevertheless, it does stress the importance of active submission for the formation of *stable* relationships of dominance and submission, because an animal can only be dominant if another submits.

I observed a similar pattern of behaviour in another clan, where a sub adult male and female were being aggressive towards a female of lower social rank. However, she responded to their behaviour by initiating play, rather than submitting. Eventually cubs started to play as well, which made it more difficult for the others to be aggressive. Again, it is not certain whether she was being tactical or genuinely 'wanted' to play (or maybe both). In both cases, subordinate females were able to diffuse aggression by the more dominant individuals and reduce tension. It appears that subordinate females have evolved a variety of strategies to avoid competitive situations with dominant females. For example, females of lower rank tend to be at the den earlier than females of higher rank, perhaps to avoid being harassed by dominant individuals. However, I did observe a high-ranking female playing with a low-ranking female for at least 30 minutes. To my knowledge, play behaviour in adult spotted hyenas has not yet been investigated in detail. However, in infant spotted hyenas, it is thought to promote affiliative relationships important for group cohesion (Drea et al., 1996). Following my observations, play behaviour seems to be important to relax the dominance hierarchy and reduce tension between adults as well as infants.

4.3 Female mating strategies (personal communication with Marion East)

Female mating behaviour may play an important role in preventing infanticide by males (Marion East, personal communication). By mating with several males, females may confuse males over paternity (see also Hrdy, 1979), which is thought to reduce the occurrence of infanticide (observed only once in 20 years in Serengeti spotted hyenas). For example, for a male to be able to assess the reproductive status of a female, males require close access to females. Females may be able to conceal their reproductive status by being aggressive to unwanted males and only allowing males that they prefer, to approach. Therefore, these preferred males have a better chance of detecting whether or not a female is able to conceive. Another way females can conceal their reproductive status is by rolling themselves in the urine of other females, leaving them with a confusing combination of hormone profiles. Contrary to what has been described in many patriarchal hierarchies; alpha males of spotted-hyenas do not necessarily produce the most offspring, and females change the father of their cubs throughout their reproductive life span.

4.4 Male Behaviour, dispersal and immigration

When males immigrate into a new clan, they no longer interact with females in the same way they would in their natal clan and spend most of their time at the periphery of the communal den area (Marion East, personal communication). Therefore, studying adult males presents more of a challenge, since their solitary and nomadic existence makes them more difficult to locate, unlike females in which most observations of individuals and their interactions can be made at communal dens. My first interesting observation of male behaviour was seeing a male being challenged by a female coalition when trying to harass a female. Although other males were present, the female coalition caused them to scatter and retreat as far as necessary from the females. However, in the reverse situation, a male challenging a female, other females in the vicinity would usually support the harassed female by chasing away the intruding male (Marion East, personal communication). In contrast to females, relatively little is known about the ways in which males communicate and organise their social relationships, however, it appears that males of similar tenure do establish social bonds. For example, I observed a

coalition of long tenured males challenging a new immigrant male that was high-ranking in his natal clan.

Male spotted hyenas appear to pose a category crisis to the conventional view of the dominant and competitive male. For example, females have priority access to food, and males rarely challenge or harass females around food resources. In spotted hyenas, males do not fight for access to females but instead express their interest in a female in various ways including shadowing (i.e. staying close to and following a female for several days). Longer tenured males usually approach females more carefully and tend to be tolerated more by females compared to short tenured males (East and Hofer, 2001). Affliliative interactions between males and females do occur, but they are less common than female-female interactions. However, males are not always so patient with females. In particular, immigrant males often harass females, especially in the absence of other females (Marion East, personal communication).

I observed males harassing females frequently in both the Isiaka and Mamba clans. However, it is not surprising that long-tenured males are more tolerant, since a short-tenured adult male that was harassing a female by repeatedly creeping up on her and biting her, was bitten very badly by the female after several warnings to which the male did not respond. Interestingly, the alpha-male, who was present at the time approached the attacked and bleeding male, and sniffed him around the mouth. Was the alpha male offering some sort of comfort? Or assessing which female he was bitten by? In any case, together my observations indicate that male-male relationships may be more complex than they seem. Thus, perhaps the 'friendly' behaviour we see in males towards other males is not only a tactic to access females but may encompass a variety of social functions in the male hierarchy, such as the maintenance of their coalition status with other males.

When reaching 2-3 years of age, sub-adult males typically leave their natal clan and immigrate into a new clan. Emigration is a gradual process and males often return to their natal clan while simultaneously trying to integrate themselves into a new one (Marion East, personal communication). There are several reasons for why males might do this. Before emigration sub-adult males are integrated in the female hierarchy and like females acquire a social rank below their mothers. Conversely, when emigrating

they have to join at the bottom of the male hierarchy, and access to females can take up to several years (Marion East, personal communication). Leaving the natal clan may induce a significant degree of stress in males. Firstly, they lose their social bonds with their relatives and other individuals and second, immigrant males need to establish new relationships in a foreign environment in which they have little or no contact with others, since the male hierarchy seems to be less bonded than female relationships, and relationships between females and their offspring. Therefore, males may benefit from occasionally returning to their natal clan, since social bonds with their former group members may help by reducing stress (though to my knowledge this has not been tested in spotted hyenas), or/and, may facilitate their access to food. Some males never leave their natal clan. For example, a male who had lost one of his forelimbs in a snare four years prior to my visit had remained a member of his natal clan. Still alive, he probably benefits from knowledge of the territory and maintenance of social bonds with clan members.

Conclusions

Following this detailed review and study on spotted hyenas, it should become apparent that androcentric views of dominance can profoundly misrepresent animal organisations that are based on female dominance, which is often expressed differently than male dominance. Focusing predominantly on assertive behaviours reinforces definitions of dominance, where an individual's social status is determined by the outcome of *agonistic* encounters (Drews, 1993). Although Drews (1993) states that one individual of the dyad must yield to be classed as subordinate, it is not a fact that relationships of dominance and submission are always established during agonistic encounters. Actually, dominance relationships do emerge in the absence of challenges (Newton-Fisher, 2004) because subordinate animals, as is the case in spotted hyenas, will habitually signal submission in the absence of a direct threat or challenge. Also, in spotted hyenas submission is not necessarily a product of one-to-one relations, even when they occur in one-to-one situations. This is because hyenas are long-lived, smart animals, and if a subordinate animal fails to submit in a one-to-one situation, it runs the risk of escalated conflict from a coalition if the animal challenging it can in the present or in the future recruit coalitional support.

Despite their highly cooperative relationships, female spotted hyenas do occasionally try to increase their social rank when an opportunity arises because higher-ranking females produce more offspring, compared to low-ranking females, as a result of spending more time in the clan territory, and having priority access to resources. Another way in which low-ranking females have improved their status is by forming a new clan, which may be possible when a neighbouring clan dies out (Holekamp et al., 1993; Höner et al., 2005). Since neighbouring hyena clans do not exclude 'intruders', commuting individuals have access to resources outside their own territory range. Thus, it appears that spotted hyenas follow paths from high resistance to low resistance, a pattern that is expected from 'ideal free distribution' (Fretwell and Lucas, 1970), which predicts that animals distribute themselves in a manner likely to provide them with the best access to resources, given the prevailing distribution of animals. In essence, this means that if the area with the maximum amount of resources is crowded, an individual may do as well or even better to go elsewhere, even if it is to an area with fewer resources. Therefore, by altering their foraging strategies, females can avoid escalated conflicts with other clan members during times of mid- and low-prey abundance, which happens to result in stable dominance hierarchies.

Finally, it has been suggested that the costs and benefits of being dominant or subordinate vary depending on the circumstances (Drummond et al., 2003). For example, in a study in blue-footed boobies (*Sula nebouxii*), Drummond et al. (2003) found that dominants and subordinates differed very little in their foraging skills and ability to compete for and defend resources such as nest sites and mates. Possible explanations for this pattern could be that subordinates, despite having clear disadvantages to dominants in some behavioural domains, are compensated by alternative advantages in other domains (Drummond et al., 2003). It would be interesting to investigate whether such alternative strengths or tactics exist in subordinate spotted hyenas. It is already known that lower-ranking females attend the communal den at different times to dominant females, perhaps to avoid harassment. Perhaps mid- and low-ranking females, that travel double the amount of distance per year on commuting trips compared to high-ranking females (see East and Hofer, 2002), are more experienced at finding food outside the clan territory compared to high-ranking females. Therefore, when low-prey availability prevails and all clan members are forced to leave the territory, low-ranking females may obtain more feeding

opportunities compared to high-ranking females. However, low-ranking females may have less energy reserves compared to higher-ranking animals, which is likely to be disadvantageous for low-ranking animals undergoing long-distance foraging trips.

Chapter 7: *Discussion and future directions*

Gina Raihani

1. Summary and interpretation of my findings

Together, these studies support my overall argument that animals have evolved remarkable behavioural adaptations that appear to both influence and be influenced by diverse contexts and intensities of competition. For instance, my studies on bustards and American rubyspot damselflies revealed a relationship between individual attributes, such as body size and condition and their mating behaviour. In bustards SSD was related to display behaviour and the intensity of male mating competition, while fat reserves in odonates influenced their 'choice' of ARB. The same pattern could be found in spotted hyenas, in that female social rank partially predicts female associations in the formation of coalitions. For example, higher-ranking females were more likely to form coalitions, compared to low-ranking females. Thus, social status appears to influence the degree of assertiveness and receptivity expressed by females.

In most cases, these similarities would be disregarded as too obvious to demand further attention. However, I argue on the contrary, that behaviour is too often undermined as a major aspect of evolutionary change and adaptation/attunement. My Chapter on spotted hyenas, which also addressed gender issues, demonstrated that scientific evidence alone or the lack it, is not always enough to transform some of our most ingrained assumptions. Therefore, I propose that a flexible model, which invokes the link between animals' circumstances (ecological, social etc...) and their behaviour, is a critical starting point for the understanding of evolutionary processes of change and adaptation from diverse perspectives.

2. Social behaviour in context

A challenge for evolutionary biology and behavioural ecology is determining how social behaviour is influenced by diverse environmental, social and individual circumstances. This becomes even more complicated when animals belonging to the same species respond to similar environmental cues in different ways. This is the case in many insect parasitoids, in which foraging behaviours may depend on their physiological state and previous experiences, or these differences may also have a genetic basis (van Alphen et al., 2003). Therefore, I explore the subtle but very important connections between my three studies by complementing them with a review,

which focuses on how these animals respond to competition based on both their dynamically bounded local (e.g. condition, individual attributes) and non-local (environmental) circumstances. Thus, I expand on my initial investigations to include some examples of how bustards, damselflies and hyenas actively attune their social behaviour with their diverse physiological, ecological and social environments.

2.1 Context-dependent behavioural flexibility in bustards, odonates, and spotted hyenas

First, in bustards I discuss the ways in which ecological circumstances, such as habitat can influence flexibility in mating systems. Similar to the alternative mating behaviours in American rubyspot damselflies, which are influenced by an individual's condition, bustards also exhibit huge flexibility in mating systems, which can vary both between and within the same population. Then I go on to explore the relationships between physiological condition and alternative mating behaviours in odonates. However, I also stress that female mating behaviours may play a more important role in the determination of male mating tactics than was previously considered. Therefore, I also explore reproductive behaviour in female odonates and the way they interact with male behaviour. Finally, I compare the foraging behaviour and group dynamics in different populations of spotted hyenas inhabiting diverse ecosystems throughout Africa, to see how these animals manage seasonal changes in prey abundance and distribution, and competition with other predators, mainly lions.

Using these examples, I hope to complement my own findings by demonstrating the variety of ways in which behaviour both influences and is influenced by diverse contexts, types and intensities of competition. I also show how our initial conceptions of 'sex-roles' can be transformed by including and interpreting the sexes, and their behaviour, within a dynamically changing ecological and social context. I propose that animals not only respond to competition, but also have a direct influence on the nature and intensity of competition. Competition should not be viewed as a process that sorts the 'fit' from the 'unfit', but rather as the source of innovation and discovery itself.

2.1.1 Ecological influences on mating behaviour in Bustards

2.1.1.1 Mating system flexibility

The underlying assumption directing the study of mating systems is that there is a degree of competition between at least one of the sexes. Unfortunately, studies describing the relationships between ecology, intra- and intersexual competition and mating systems in bustards are relatively scarce. However, it is well known that polygyny is more frequent in some habitats, compared to others (Verner and Willson, 1966). Emlen and Oring (1977) analysed various ecological variables that influence the type and intensity of competition in polygamous mating systems and provided a framework for predicting mating systems based on ecological factors. They suggested that spatial and temporal resource dispersion is an important predictor of mating system. For example, polygamous mating systems are more common when critical resources are unevenly distributed. This is because some individuals may be able to defend a larger quantity or better quality of resources compared to others, leading to substantial differences in reproductive success between competing individuals. Furthermore, when resources become clumped, the intensity of sexual selection is likely to increase even more as a small percentage of the population can potentially monopolise a large proportion of available resources.

However, the intensity of intramale competition can increase even more when females in a population reproduce asynchronously leading to a heavily skewed operational sex ratio (average ratio of fertilisable females to sexually active males). In this scenario, males often aggregate solely for the purpose of courting and attracting females (lek mating system). Emlen and Oring (1977) proposed that a lekking system is expected when breeding seasons are long, the operational sex ratio is heavily skewed, and when males are unable to monopolise resources critical to females, which influences the intensity of sexual selection. However, polygamy can also depend on other factors, such as the ability of one of the sexes to provide full care for their offspring. Also, in polygynous birds, habitat requirements may differ between the sexes, especially during the breeding season, which is also likely to influence mating systems (Emlen and Oring, 1977). Emlen and Oring (1977) concluded that ecological variables impact the intensity of sexual selection, which in turn is likely to influence the type of resulting mating

system. Therefore, it is not surprising that animals exposed to unpredictable and changing environmental circumstances, such as differences in the dispersion of critical resources or the availability of mates, have evolved a degree of flexibility in their mating systems. Thus, shifts in mating behaviour are likely to be related to changes in intra-male competition associated with differences in energetic costs of mate or resource defence (Emlen and Oring, 1977).

The increasing influence of behavioural ecology has resulted in more data and theoretical models that acknowledge the flexibility of mating behaviour in some species and the degree of intraspecific variation in mating systems (Lott, 1991). Therefore, rather than viewing mating systems as fixed, nowadays scientists classify mating systems based on female and male patterns of spatial and temporal dispersion, and patterns of parental care (for a review on avian breeding systems see Ligon, 1999; Bennett and Owens, 2002). In this section, I focus on polygynous mating systems in bustards with a special focus on resource-based polygyny and exploded lek mating systems. In these mating systems, environmental influences are likely to play a more important role, compared to classical lekking species, since the former are more sensitive to variations in resource availability.

2.1.1.2 Mating system flexibility in bustards

Most bustard species have a polygynous mating system, while all five species belonging to the genera *Eupodotis* are considered to be monogamous (see Chapter 4). Lekking behaviour was initially documented only in the Great bustard (Höglund and Alatalo 1995). In a classical lek (for a review on lekking behaviour see Höglund and Alatalo 1995), males gather at a similar site to compete with other males and court females who visit leks to choose mates. In this system, males do not provide females with resources and do not participate in parental care. Only the Great bustard exhibits classical lek behaviour, however, most other species show exploded leks (see Morales et al., 2001), in which males display in large territories and at large distances apart. However, owing to a degree of intraspecies variation in mating systems (Carranza et al., 1989; Collar et al., 1996), defining a set of species-specific mating systems in bustards can be complicated. Such intraspecific variation suggests that ecological and/or social factors may be influencing mating systems. If this is the case, then flexible mating behaviour

might be expected in species that are subject to unstable or changeable environments (e.g. Great Bustards: Carranza et al., 1989). To explore this, Carranza et al. (1989) investigated the relationship between a number of ecological variables and the outcome of different mating strategies in the Great Bustard (*Otis tarda*). They found that observed changes in mating system are associated with changes in weather conditions, changes in timing of mating, diet and social factors. Social parameters in particular appear to be influential in Great Bustards, since conspecific attraction, rather than the suitability of available habitats, appears to determine preferred sites (Lane et al., 2001).

In a two-year study in the little bustard (*Tetrax tetrax*) in France, Jiguet et al. (2000) fully investigated their mating system, which is considered to fit the criteria of an exploded lek. In this bustard species, males are clustered at display areas in relatively large territories, and do not care for their offspring (Schulz, 1985). To determine whether the little bustard can be regarded as a lekking species, Jiguet et al. (2000) investigated two important requirements for their mating system: male aggregation in arenas, and the absence of consistent resources in male territories. For this, they explored the spatial distribution of male territories, individual variation in territory size, and habitat characteristics of male territories. As predicted, displaying male little bustards did aggregate at display sites, which did not appear to be related to habitat limitations because males were absent from many areas with abundant permanent crops. However, in other populations, little bustards do not cluster on lek arenas, and defend resources valuable to females (Höglund and Stöhr, 1997). Second, male territories were relatively large, though individual males did show a large variability in territory size.

The habitat used by males reflected a balance between male nutritional needs and display cover, rather than female requirements. For example, males avoided cereal and rapeseed crops in the breeding season, because they grow too high in the spring and thus obscure the visibility of males whilst displaying. However, it appears that some males defended large territories to accommodate suitable nesting areas for females. Jiguet et al. (2000) concluded that little bustards do generally fit the criteria of leks, however, some populations show exceptions to this rule, which may be caused by environmental influences such as density, sex-ratio or habitat quality. Therefore, Jiguet et al. (2000) proposed that little bustards are best described as exhibiting a continuum in mating behaviour, ranging from resource defence polygyny, to resource-based or

exploded leks.

A similar study looking at habitat use and mating systems was conducted in houbara bustards (*Chlamydotis undulata undulata*), which have a polygynous mating system that is thought to resemble either an exploded lek or resource defence polygyny (Hingrat et al., 2007). Using arthropod biomass as an indicator of trophic quality in six habitats, Hingrat et al. (2007) investigated whether sexual and seasonal variations in habitat use were associated with resource availability. They also tested whether males defended crucial resources for nesting females.

Their results demonstrated that males and females differ in their spatial and seasonal patterns of habitat use, which is related to sex-specific reproductive needs and social organization. First, males and females differed in habitat selection during the breeding season in winter and spring, but foraged together with juveniles in the non-breeding season in autumn and summer. Also, habitat type selection was constant in males, but highly variable in females, which is thought to be linked to the high variation in behaviour demonstrated in the female annual cycle that includes a mating or pre-laying period, nesting period, and brooding period, each with diverse habitat requirements. Similar to little bustards, habitat selection by males did not solely reflect food availability, since males remained faithful to display sites even in the non-breeding season. This stresses the importance of display site selection in determining patterns of male distribution. Females did appear to select habitats where food resources were abundant, including regular and tall perennials in spring, which help conceal chicks from prey such as foxes.

Hingrat et al. (2007) concluded that owing to the considerable differences between the sexes regarding habitat preferences, the mating system of the Houbara Bustard fits the criteria of an exploded lek, since males do not appear to defend critical resources used by females. Nevertheless, the criteria that fulfil the definition of a mating system, such as the exploded lek, must always be treated with caution, since it is difficult to determine whether these relatively large male territories (compared to classical leks) contain resources valuable to females and/or their brood. A reason for this may be that the spaces between males provide necessary resources for males, or nesting habitats for females (Hingrat et al., 2007). Therefore, it is not surprising that exploded or resource-

based lek species show more intra-specific variations in their mating systems compared to classical leks (Jiguet et al., 2000).

In conclusion, the study of mating systems offers valuable insights into evolutionary processes that drive the evolution of novel adaptations and speciation. Many hypotheses have been proposed to explain the flexibility of mating systems, including ecological variables (discussed above), patterns of parental care, and life histories (Bennett and Owens, 2002). For example, species whose life-histories are characteristic of high mortality and high annual reproductive rates are more likely to exhibit a type of polygamous mating system, extra-pair paternity, and intraspecific brood parasitism (when females lay their eggs in the nests of other females). Interestingly, mating systems can also be affected by correlated behaviours across different contexts: i.e. behaviours in non-mating environments that affect behaviours in mating situations. For example, male sticklebacks (*Gasterosteus aculeatus*) that are more assertive towards predators are better at obtaining breeding sites (Huntingford, 1976). Therefore, owing to this large degree of flexibility in behaviour, animals can adjust their mating behaviours in a manner that fits a huge array of environmental circumstances. However, determining how these interact to influence the evolution of mating systems and distinguishing between the causes and consequences of social behaviour remains an ongoing challenge for biologists, which calls for an integrative approach for the study of mating behaviour.

2.1.2 The influence of condition on mating tactics in odonates

This section follows from the last by expanding from the ecological variables that influence social behaviour to include how social behaviour is affected by an individual's 'state' or condition. Thus, in many animals, mating behaviours cannot be predicted solely by the spatial or temporal distribution of resources (mating or non-mating), but rather on an animal's individual attributes such as morphology (e.g. bustards: see Chapter 4; Austed, 1984; Dominey, 1984; Emlen, 1997; Lidgard et al., 2005), or condition (Dunbar, 1982; Gross, 1996, McNamara and Houston, 1996). For example, in male grey seals, body size determined male mating tactics (Lidgard et al., 2005). Interestingly, despite larger males having a greater energetic advantage and an endurance advantange, males of intermediate body size had the highest reproductive

success, presumably because their enhanced agility was advantageous during male-male combat. Both large and intermediate males exhibited the primary tactic of consortship while smaller males with the lowest reproductive success engaged in a non-consortship tactic. Therefore the authors suggested that stabilising selection might be influencing male body size in seals towards a size that is large enough to adopt the primary mating tactic, but not too large, which limits agility.

Life history theory is often used to predict when and how much an organism should reproduce throughout its lifespan (McNamara and Houston, 1996). Thus, depending on the relative costs and benefits of reproductive investment, an individual should adopt reproductive behaviours that maximize their fitness. For example, in matrilineal hierarchies in which daughters acquire a social status just below their mothers, social status is often positively correlated with a females' ability to gain access to resources, which is in turn correlated with the reproductive success of the female and her offspring (McNamara and Houston, 1996; see also Chapter 6). Thus, from a life history perspective the amount of effort that an individual invests in maintaining their social status should reflect the relative benefits they receive in terms of reproductive success. Therefore, high-ranking females in spotted hyenas invest more time and energy in cultivating strong social bonds to secure coalition partners, since the reproductive costs associated with dropping in social rank are considerably higher for high-ranking females, compared to low-ranking females (see Chapter 6).

2.1.2.1 Female reproductive behaviours

Although these examples clearly show that condition, size or rank influences social behaviour, they do not explain how such diverse behavioural tactics evolved. I suggest that to understand why territoriality evolved in odonates, we need to look at the reproductive behaviour of females as well as males and how their interactions have led to the evolution of territorial and non-territorial tactics in male odonates. In most odonates (Zygoptera in particular) males cannot mate with females without their full cooperation, since the female must raise her abdomen before the male can engage his genitalia (Fincke, 1997). Also, life begins under water in odonates at the sites where females lay their eggs (Corbet, 1999). Thus, it is typically at riverine sites where mating and oviposition takes place.

Reproductive behaviour has been studied in detail in Calopterygid damselflies (Córdoba Aguilar and Cordero Rivera, 2005). In these species males defend territories, which females visit for the purpose of mating but do not necessarily lay their eggs in the territories of mated males. In some Calopterygids, territorial males demonstrate up to 1000 times the mating success compared to non-territorial males (however this can change depending on population density: Cordero, 1999), since females mate predominantly with territorial males (Plaistow and Siva-Jothy, 1996). Therefore, could such female preferences have influenced the evolution of male territorial behaviour in odonates?

Interestingly, most odonates basal in the phylogeny exhibit non-territorial behaviour, while more recent species have a tendency towards territoriality (A. Cordoba Aguilar, personal communication). Therefore, since non-territorial males usually lack courtship and attempt to gain access to copulations by actively searching for females or sneaking (for a review of non-territorial behaviours see Corbet, 1999), territoriality in males may have evolved in response to female preferences for male site fidelity. Perhaps the difficultly for males to locate females in certain species (e.g. in *Hetaerina americana*, see Chapter 5), promotes male territorial behaviour, since they stand a better chance waiting for females to visit them. However, this hypothesis has not been investigated in odonates, which requires more data on long-term mating patterns in females. Also, male territoriality may be beneficial for females, because it appears to provide females with more control over which males they choose to mate with.

However, female mating behaviour and its relationship with male mating behaviour has to my knowledge not been investigated in odonates. The benefits of female choice are likely to be the greatest in those species or populations in which males must endure huge physiological challenges (associated with territory defence) in order to gain mating opportunities (Fincke, 1997). For example, territorial males in *Calopteryx*, *Neurobasis, Vestalis* and *Mnais* species exhibit elaborate courtship displays (see review in Córdoba Aguilar and Cordero Rivera, 2005). In *Calopteryx splendens*, for instance, females preferred to mate with males that were able to defend sites with a certain river flow rate, which has been shown to decrease the chances of eggs being infected with fungi (Siva-Jothy et al., 1995).

2.1.2.2 The evolution of condition-dependent ARBs

Given that territorial and non-territorial behaviour has evolved as alternative mating behaviours in odonates, what influences the type or types of mating tactics that an individual adopts? Odonates are ideal for investigating alternative reproductive tactics, since males exhibit a range of territorial and non-territorial behaviours, which owing to their huge variability are better understood as a continuum rather than fixed categories (Corbet, 1999). Here, I investigate how odonates respond to their condition by adopting alternative mating tactics.

Mating tactics that appear to be influenced by age often reflect underlying physiological factors (e.g. the damselfly *Calopteryx maculata*: Forsyth and Montgomerie, 1987). Forsyth and Montogomerie (1987) initially found that male mating tactics were correlated with age, with younger males usually adopting a territorial tactic but switching to sneaking behaviour as they got older. The authors concluded that the tendency of males to adopt an alternative mating tactic as they got older reflects the huge energetic demands associated with territoriality. This non-territorial tactic appeared to have increased lifetime reproductive success in males that were no longer able to defend territories. However, territorial males still obtained significantly more matings per day compared to non-territorial males. As a consequence of the high energetic requirements for territorial males, males are usually larger than females and fat reserves are critical for the ability of males to defend territories. This also holds true in species such as Calopterygidae, in which males exhibit both territorial and non-territorial mating tactics. The latter tactic is usually adopted when a male gets older and no longer has the energy reserves necessary for winning territorial contests (see Córdoba Aguilar and Cordero Rivera, 2005).

Nowadays it is well established in many damselflies (in particular Calopterygid species) that fat reserves play a critical role in determining which males win contests over territories (Marden and Waage, 1990, Plaistow and Siva-Jothy, 1996; Koskimäki et al., 2004; Serrano-Meneses et al., in press), as well as the availability of riverine sites (Pajunen, 1966). Thus, a possible reason for why larger males are often successful at gaining territories is the fact that larger males can store more fat reserves, compared to

smaller males (e.g. *Calopteryx xanthostoma:* Plaistow and Siva-Jothy, 1999). In *Calopteryx splendens xanthostoma*, fat reserves reflect a male's age, which in turn is an indicator of how long he has been defending a territory. Thus, young pre-territorial males had the most amount of fat reserves, territorial males that had gained a territory had intermediate fat reserves, while older, displaced males had extremely limited fat reserves (Plaistow and Siva-Jothy, 1996). It has been found that larval diet affects the amount of fat reserves at emergence: Larvae reared on a low-nutrition diet were significantly smaller at emergence with less flight muscle mass and fat reserves compared to those reared on a high nutrition diet (Plaistow and Siva-Jothy, 1999). However, there was no difference in the development rate or survival between the two diet regimes. This suggests that developmental time is the main determinant of fitness and is thus maintained at the expense of body size and investment in fat reserves and flight muscle (Plaistow and Siva-Jothy, 1999).

2.1.2.3 Genetically-based ARBs

Mnais species are an exception amongst the Calopterygids, since mating tactics have a genetic basis resulting in two morphologically and behaviourally distinct morphs (Tsubaki, 2003). In *Mnais costalis* territorial males are termed orange-winged 'fighter' males, while non-territorial males are clear-winged 'sneakers'. Firstly, orange-winged males and females gained almost double the mass between eclosion and reproduction compared to clear-winged males, in which development is less costly. Thus, reproductive costs in orange-winged males and females led to a decrease in adult fat reserves with age, while fat reserves in clear-winged males remained constant throughout their lifespan. This higher investment by orange-winged males may explain why body size influences their mating success, while body size had no effect on the mating success in clear-winged males (Plaistow and Tsubaki, 2000). Lifetime reproductive success for the two morphs was equal, despite orange-winged males having a shorter reproductive lifespan and longevity compared to clear-winged males (Tsubaki et al., 1997).

Plaistow and Tsubaki (2000) suggested that the occurrence of the two morphs is more likely to be the result of different selection pressures acting on each morph, rather than

by phylogeny or habitat, since orange-winged and clear-winged males experience similar phylogenetic constraints and occur in the same environments.

Furthermore, these different selective pressures acting on the two morphs and females result in different developmental costs: the two morphs and females were similar in weight at eclosion, but females and orange-winged males gained double the amount of mass during the pre-reproductive stage compared to clear-winged males, which supports the hypothesis that mass gain in orange-winged males is an adaptation for territoriality. This was further supported by the finding in orange-winged males and females that flight muscle and fat development was affected by nutrition, again, not a relationship found in clear-winged males. In conclusion, orange-winged males demonstrated the most costs of development, which declined considerably in low nutrition environments (Plaistow and Tsubaki, 2000).

2.1.2.4 Condition-dependent female ARBs

Finally, condition can also affect female reproductive decisions. For example, female mating behaviour in *Calopteryx haemorrhoidalis* is influenced by parasite burden (Córdoba-Aguilar et al., 2003). In this species, males typically defend riverine territories, in which females oviposit their eggs while guarded by the copulating male against potential intruders. However, females that do not mate with a territory holder may nevertheless 'steal' an oviposition site located in his territory. Similar to males, females also have wing pigmentation, which is negatively correlated with their number of gut parasites. Females with fewer gut parasites were courted for longer, visited more males, were more selective towards highly pigmented males, and had higher mating success. However, females with a larger amount of gut parasites produced fewer eggs, survived for fewer days, spent less time in courtship and inspected fewer males prior to mating, were guarded for less time during oviposition, and had lower mating success.

Therefore, the decline in reproductive investment in infected females may be a strategy that partially compensates for their lower survival rates. Also, less parasitised females were more likely to steal oviposition sites from territorial males compared to more parasitised females. The reason for this may be explained by differential sperm use by females, which has been studied in a closely related species: *C. splendens xanthostoma,*

in which unguarded females use a diversity of male sperm stored in their spermatheca for fertilising their eggs (Siva-Jothy and Hooper, 1995). However, when males guard females during oviposition, only the sperm from the last mated male is used (Siva-Jothy and Hooper, 1996). Córdoba-Aguilar et al. (2003) concluded that this might well also apply to *Calopteryx haemorrhoidalis* females, who appear to adjust their reproductive behaviours according to their condition. Thus, less infected females that mate multiply with high-quality males, may benefit more from differential use of sperm compared to infected females that mate with fewer and lower-quality males. This may be due to infected females having less opportunity to invest in reproduction (i.e. mate solely with high-quality males), compared to uninfected females.

2.1.3 Prey availability and its effect on foraging behaviour in spotted hyenas

So far we have seen how reproductive behaviour is manifested and manifests itself in different environmental, social, morphological and physiological contexts. However, the examples I have given so far have only focused on how *individuals* respond to changes in their circumstances. In group-living animals it becomes even more complicated because the costs and benefits associated with the actions of one individual, depends on the way it affects social bonds and cooperative relationships with other group members. Here, I will describe the differences in foraging behaviours between spotted hyena populations living under different ecological circumstances. However, despite these differences in foraging strategies between groups, all spotted hyenas live in stable clans (Kruuk, 1972) and have a female-dominated matrilineal social system (Frank, 1986b). This highlights the importance of considering other explanations as well as purely adaptive ones for the evolution of social behaviour, which I will discuss in more detail later on.

In the Serengeti ecosystem, which is dominated by migratory herbivores, food in the clan territory can get so low that individuals temporarily leave the group to forage alone and avoid competition with other group members. Also, spotted hyenas tolerate the presence of 'intruders' from neighbouring clans when there is a superabundance of food in their clan territories (Hofer and East, 1993a), which facilitates the commuting system. Therefore, Serengeti spotted hyenas can support large groups similar to those found in the Ngorongoro Crater, which is dominated by resident herbivores (Kruuk, 1972; Hofer

and East, 1993a). Therefore, this suggests that the foraging ranges in Crater and Serengeti spotted hyenas are decoupled from clan territories, and clan sizes are not restricted by the abundance of prey within clan territories (Hofer and East, 1993a,b). Conversely, lions show much lower densities in the Serengeti compared to the Ngorongoro Crater, which is due to the year-round availability of food in the Crater. However, the higher densities of lions in the Ngorongoro Crater ecosystem was associated with high injury costs, due to territorial disputes between residents and intruders (Heinsohn, 1997). These differences in the social and territorial behaviours between spotted hyenas and lions, thus leads to different consequences for their group sizes and intraspecific competition.

Although the commuting system is specific to Serengeti spotted hyenas, other spotted hyenas living in diverse ecosystems also exhibit flexible territorial conventions. I propose that this flexible behaviour in spotted hyenas reflects their ability to exploit prey throughout the year. Trinkel et al. (2004) investigated the spatial behaviour of spotted hyenas in different ecosystems to see how differences in prey abundance and distribution may affect territory size, clan size, and foraging strategies in different spotted hyena populations. They found that spotted hyena clans living in ecosystems with resident herbivores maintain permanent territories, since prey remains constant throughout the year. In contrast, Etosha (Trinkel et al., 2004) and Serengeti spotted hyenas (Hofer and East, 1993a) that are subject to large fluctuations in prey availability, due to their dependence on migratory herbivores, need to adjust their spatial behaviour in a way that they can access food throughout the year. For example in the Etosha National Park, Namibia, spotted hyenas enlarged their clan territories up to double the size in the wet season when migratory herbivores moved North-West from their clan territory. Therefore, Etosha spotted hyenas responded to the decline in density of prey in the Etosha National Park by expanding their territories to follow migratory prey.

Given that both Serengeti and Etosha hyenas have to deal with fluctuating levels of prey, then why have they evolved different strategies for coping, and why are Etosha clan territories much larger than those in Serengeti spotted hyenas? As described in Chapter 6, Serengeti spotted hyenas maintain permanent territories but forage outside their clan when prey gets too low to sustain all clan members. Trinkel et al. (2004) proposed an explanation for the observed differences between Serengeti and Etosha

spotted hyenas based on differences in their concentrations of migratory herbivores. In the Serengeti, commuting spotted hyenas are exposed to high densities of migratory herbivores in the Northern woodlands during the dry season, and again in the southern plains during the wet season. Etosha spotted hyenas on the other hand only experience higher densities of herbivores during the dry season (though significantly lower than Serengeti hyenas when prey availability is at its highest: see Table 1; taken from Trinkel et al., 2006). During the wet season, migratory prey was highly dispersed, thus Etosha hyenas need to expand their territories in order to meet their food requirements (Trinkel et al., 2004). The Kalahari spotted hyenas face the greatest challenges for finding food, owing to their desert ecosystem in which prey are dispersed unpredictably and are at extremely low densities (see Table 1). Thus, in these areas clan territories can reach up to 1800 km^2 (Mills, 1984).

Table 1 Spotted hyena clan sizes, territory sizes, migratory and resident prey densities d_m, d_r and prey availabilities p_m, p_r in different ecosystems

Label in Fig. 1	Ecosystem	Clan size	Territory (km^2)	d_m	d_r	p_m	p_r	Reference
1	Hluhluwe	9	13	0	46	0.0	18.4	Whateley & Brooks, 1978
2	Kruger	11	130	0	12	0.0	12.4	Henschel, 1986
3	Kalahari	9	1095	>0[a]	3	0.0	11.0	Mills, 1984
4	Ngorongoro	54	30	0	95	0.0	9.6	Kruuk, 1972
5	Masai mara	52	60	4	52	0.6	7.8	Frank, 1986
6	Namib Desert	4	570	0	1.2	0.0	7.2	Tilson & Henschel, 1986
7	Serengeti 1	47	55	3.4	3	0.6	0.5	Hofer & East, 1993
8	Serengeti 2	47	55	28	3	4.4	0.5	Hofer & East, 1993
9'	Etosha 0	14	160	1	1	0.9	0.9	Trinkel *et al.*, 2004
9	Etosha wet	14	320	5	1.2	6.4	1.3	Trinkel *et al.*, 2004
10	Etosha dry	14	160	12	1	11.2	0.9	Trinkel *et al.*, 2004
11	Serengeti 3	47	55	240	3	37.4	0.5	Hofer & East, 1993

[a]Infrequent wildebeest migration, no actual numbers for prey density were found.

2.1.4 Kleptoparasitism and competition with lions

Another problem facing many spotted hyenas, apart from the challenge of exploiting migratory prey throughout the year, is the presence of other predators, in particular lions (*Panthera leo*), whose diet overlaps with that of spotted hyenas (Kruuk, 1972). In spotted hyenas interspecific Kleptoparasitism can either pose a problem (Trinkel and Kastberger, 2005) or offer a solution (Höner et al., 2002) to a decline in food abundance. Although spotted hyenas are efficient hunters, and acquire most of their food by hunting, they can also scavenge (Kruuk, 1972). In the last three decades, Ngorongoro Crater spotted hyenas have experienced a significant decline in the number of their main prey species, and an increase in buffalo (*Syncerus caffer*), which was rarely hunted (Höner et al., 2002). Therefore, by comparing data on feeding ecology from the late 1990s (period 2) and the late 1960s (period 1), Höner et al. (2002) investigated how spotted hyenas respond to long-term changes in prey populations.

Their results confirmed their prediction that spotted hyenas do exhibit a functional response to a long-term decline in their preferred prey species, since spotted hyenas in the Crater hunted adult wildebeest and buffalo calves during period 2, which were rarely hunted during period 1. However, adult buffalos were hunted less often than expected, presumably because they are extremely difficult for spotted hyenas to kill. Therefore, spotted hyenas actively responded to changes in prey populations by switching to prey that they previously did not pursue, but were nevertheless easy to hunt

(Höner et al., 2002). Furthermore, spotted hyenas scavenged more carcasses during period 2 compared to period 1. The fact that the concentration of buffalo increased from period 1 to 2, along with a decrease in those prey preferred by spotted hyenas, may explain why the proportion of lion kills, relative to hyenas, increased from period 1 to 2, which also led to hyenas obtaining more food by kleptoparasitising lions. Overall there was an increase in the amount of food hyenas obtained from lion kills relative to the amount of food lost to Lions from period 1 to 2. Höner et al. (2002) observed that Crater hyenas could successfully monopolise a lion kill if they outnumbered female or sub-adult lions by at least three times, provided that adult males were absent from the kill.

The authors concluded that an important factor determining the success or failure of kleptoparasitism by hyenas at lion kills, is firstly, the ratio of the number of hyenas to the number of female or sub-adult lions at the lion kill, and second, the presence of male lions, who prevent hyenas from stealing their kills. The third important requirement is the ability of hyenas to recruit enough individuals to challenge lions. Interestingly, in a study on Chobe (Botswana) spotted hyenas, Cooper (1991) estimated that the mean ratio of hyenas to Lions, in which hyenas could successfully acquire kills from lions, is 3.7. Conversely, in Crater hyenas the mean ratio is 6.8 hyenas for every lion, when a takeover occurred. Höner et al. (2002) suggested that this difference could have two possible explanations. First, Crater hyenas may be more successful than Chobe hyenas in recruiting more hyenas to lion kills. Or, Crater hyenas may require a higher ratio of hyenas to lions for stealing kills compared to Chobe hyenas. However, Crater hyenas were able to acquire 100% of lion kills in the absence of adult male lions, whereas Chobe hyenas were only able to take over 27% of these kills. Therefore it is most likely that Crater hyenas are more successful at recruiting other members, and their ability to take kills from lions did not depend on the number of female and sub-adult lions present.

Finally, Etosha spotted hyenas almost present the opposite scenario to Ngorongoro Crater hyenas, since they are both unable to take kills from lions and prevent their kills from being taken by lions (Trinkel and Kastberger, 2005). Although encounters between hyenas and lions were extremely rare (only 11 observed encounters in the1250 observation hours spread over 1 year), in seven of the observed encounters, lions took

over hyena kills, and in the other four cases hyenas challenged lions at their kills but were unsuccessful. The mean ratio of hyenas to females and sub-adult lions was 3.6. Therefore, a possible reason for why hyenas failed to take food from lions and prevent their kills being taken may have been due to the presence of male lions during these encounters, as well as the low ratio of hyenas to other lions. Also, Etosha hyenas were unsuccessful at recruiting enough clan members to challenge lions. However, this may be explained by their small clan sizes and large territories, in which only 11 individuals defend a territory over 300 km^2 (Trinkel et al., 2004).

This, contrasts strongly with Crater hyenas, in which hyenas live in large clans on small territories (see Trinkel and Kastberger, 2005). Furthermore, a striking 71% of hyena deaths were caused by lions, which presumably kill hyenas to reduce food competition (Trinkel and Kastberger, 2005). However, in response to this threat, Etosha hyenas challenge lions with aggressive behaviour in the absence of food, which is known as mobbing behaviour (Kruuk, 1972). This typically occurred when lions were close to the communal den of hyenas, which may function to deter lions away from the communal den and their cubs, and thus to avoid attacks. Also, the excitement may communicate as a warning to cubs to hide in the underground burrows.

In conclusion, foraging behaviours in spotted hyenas and kleptoparasitism provide yet another example of the ability of organisms to attune with changing circumstances. However, how can all these examples be integrated into a coherent evolutionary framework? Neo-Darwinian evolution relies on the primacy of the genotype in directing evolutionary change. However, can selection operate on environmentally induced behaviour, in which environmental effects on behaviour or phenotype appear to precede genetic influences?

3. Phenotypic plasticity: A future direction for the study of animal behaviour?

3.1 Beyond the objectivist paradigm

By studying species belonging to different taxa, I was able to explore how competition in diverse biological, social and ecological settings can influence and be influenced by the social behaviour of animals. These studies and my examples above have

demonstrated that competition, either over food or reproduction, can contribute to the generation of diversity on three distinct scales of organisation: 1) differentiation between the sexes, 2) differentiation within the same sex and 3) differentiation between groups. However, to understand how such diversity in behaviour and morphology evolves, we first need to look at how organisms relate with their environment or individual circumstances, which creates particular contexts and intensities of competition (as described in the above sections). Then, given the assumption that there is competition over resources between individuals, we can focus on the way animals respond to such competition.

Being an extremely talented natural observer, Darwin was much aware of the importance of the relationship between the organism and its environment, and his writings reflect a sense of meaning and intention regarding the way animals behave and relate with one another (Crist, 1998). However, the naturalistic writings by Darwin contrast with early scientific accounts of animal behaviour in classical ethology. Here, the study of animal behaviour became increasingly detached from studying the intentions and motivations of animals, and was replaced with a purely mechanistic view of animals, in which behaviour is determined by interior states and external stimuli (Crist, 1998). This trend can be traced back to Konrad Lorenz and Nikolaas Tinbergen, the founders of ethology, who first applied theoretical and technical models to comprehend the behaviour of animals (Crist, 1998). Without denying the great value of these models for scientific progress, a shift away from understanding animal experiences in their own world became increasingly evident (e.g. see Hediger, 1964).

Early ethologists like Lorenz and Tinbergen were under increasing pressure to justify the study of animal behaviour as a rigorous science, and thus adopted a technical language that suited the expectations of modern academia (Crist, 1998). It is unlikely therefore, that ethologists were aware at the time that this change in language would result in a different perception of animals (Crist, 1998). However, nowadays, especially in the field of behavioural ecology, most scientists do view animals as distinct subjects that relate with their environment, as well as cognitive objects.

Although we understand a great deal about the evolutionary processes that guide individual behaviour and group dynamics, less is known about the relationships between these distinct levels of organisation, and many of the proposed explanations remain highly debateable (e.g. see Chapter 1, where I discuss the evolution of cooperation). In particular, I am interested in how individuals relate with their ecological and social environment in a way that maintains fitness gradients in natural populations. Therefore, I begin by critiquing the conventional view of fitness before discussing fitness gradients and how they are maintained in populations. Here, the main argument is that fitness is context-dependent, rather than a fixed state, which ranks individuals from 'superior' to 'inferior'.

3.2 A re-interpretation of Darwinian Fitness

There is an ongoing debate in evolutionary biology regarding the way in which we measure and apply fitness concepts to evolutionary biology (Ariew and Lewontin, 2004). The most commonly used measure of fitness is the life-time production of offspring (Kozlowski, 1993), which includes the components: viability (survivorship to sexual maturity), mating success (the number of mates), and fertility per mate (the average number of zygotes produced per mate), all of which are thought to comprise the total fitness of an individual (Arnold and Wade, 1984). However, Ariew and Lewontin (2004) criticised the concept of Darwinian fitness, in particular the primacy of specifically *genetical* models of evolution under natural selection, in which ecological and demographic details are ignored. They argue that these measures are unable to predict the direction of evolution that arises from the relationship between organism and environment, and that the confusion about fitness is the result of an assumption that Darwinian fitness can be measured using a single ordinal scalar (i.e. number of offspring that reproduce), which predicts the relative increase or decrease of a genetic type. Ariew and Lewontin (2004) describe why a single ordinal scalar cannot accurately represent an individual's fitness. One reason being that fitness can also depend on the frequency of a genetic type in a population, as in the well known cases of butterfly mimicry, in which rarer types have an advantage.

Although Darwinian fitness can be a useful tool for measuring lifetime reproductive success in individuals, fitness also depends on the fit between the organism and its

environment, which can lead to huge variability in lifetime reproductive success. Therefore, it is important to distinguish whether reproductive success is the cause or the consequence of fitness.

3.3 Behavioural Plasticity/Flexibility: survival of the fitting?

3.3.1 The problem of the conventional logic of competition for explaining diversity

A large number of studies on sexual selection have demonstrated that females often favour the most vigorous, 'high quality' males, which has led researchers to study the implications of being a 'high quality' or 'low quality' male (see reviews on sexual selection: Andersson, 1994; Arnqvist and Rowe, 2005), and a huge variety of characteristics that are advantageous for males when competing for females have been identified (Kodric-Brown and Brown, 1984). For example, it has been suggested that female seals induce males to compete by protesting against unwanted males that attempt to mate with them. This attracts the attention of surrounding males, which then attempt to displace the mounting male (Cox and LeBoeuf, 1977). In the latter scenario, those males with the best fighting ability have a clear advantage.

This differential fitness has led biologists to study the implications of being a high quality or low quality individual. A large number of studies have now demonstrated that high quality individuals usually out-compete or are better adapted than low quality individuals (e.g. see: Møller and Alatalo, 1999; Jennions et al., 2001). However, few studies have emphasised the way in which low quality individuals overcome such disparity in competition leading to the paradox that if high quality individuals are able to out-compete low quality individuals, then the overall frequency of high quality individuals should exceed the overall frequency of low quality individuals in a population. This, however, is not always the case, since low quality individuals are not eliminated from populations.

From where does this paradox arise? Perhaps the over-emphasis of 'genic Darwinism' (Avital and Jablonka, 2000), has led to the perception of organisms and their individual genes as increasingly detached from the context in which they find themselves. Therefore, in the case of the lek paradox (see Chapter 1), it is generally assumed that the

full resolution can only be found in the quantification and exact knowledge of particular genes (e.g. see Kotiaho et al., 2001). Without denying the importance of genetic variation for the evolution of behaviour, the gene-centred approach is nevertheless restrictive, especially when trying to understand how nearly genetically identical individuals can exhibit striking phenotypic variation. This is because this neo-Darwinian approach depends on genetic variation, caused by random mutations as the source of new selectable variation (West-Eberhard, 2005). Therefore, genotypes rather than phenotypes are thought to be directly responsible for reproductive success.

Despite the wide acceptance of the neo-Darwinian approach, it does create problems when explaining the evolution of novelty, since it uses a concept of selection, which requires genetic variation prior to adaptation/attunement. Therefore, in the neo-Darwinian paradigm, the source of novelty must be genetic in nature as it depends solely on the variation produced by random mutations (West-Eberhard, 2005). However, West-Eberhard (2005) argues that this approach is flawed, since the ability of genes to be propagated depends on how they are expressed by and affect the phenotypes which carry them. Thus, selection should be seen as acting directly on phenotypic variation, whether or not it has a genetic basis. West-Eberhard's (1989, 2003) synthesis of evolution thus strengthens an over-looked aspect in the neo-Darwinian model, by arguing that the genotype can respond to selection on phenotypes. Therefore, West-Eberhard (2005), concluded that 'genes are probably more often the followers than leaders in evolutionary change.'

3.3.2 Phenotypic plasticity

According to the emerging theory of phenotypic plasticity (see review: West-Eberhard, 2003; but for similar arguments also see: Stenlid and Rayner, 1989; Rayner, 1997), organisms are able to express alternative morphological, behavioural and physiological characteristics in response to their environmental circumstances, which may be reflected in flexible behaviour that occurs in a matter of a few seconds, or a developmental switch that permanently fixes the adult form (Price, 2006). For example, the results from a study on two populations of European grass snakes, which differed in adult body size and the degree of SSD, suggest that prey availability had a direct effect on the morphologies without the influence of genetic modification (Madsen and Shine, 1993).

An example of environmentally induced plasticity in behaviour is nicely demonstrated by a study on bonnet macaques (*Macaca radiata*), in which adult females of different dominance rank were able to change between foraging naturally and feeding on provisioned food when provided with the alternatives. Also, when feeding competition was increased by the provisioned food, females adopted behaviours aimed at reducing the higher levels of aggression. Female bonnet macaques living in unimale groups also respond to limitations in mating opportunities by emigrating to neighbouring unimale or multimale groups (Sinha, 2005).

Phenotypic plasticity can be explained by the Baldwin effect, which was proposed over a century ago (Baldwin, 1896). Baldwin proposed three ways (he termed these ontogenic agencies) in which animals can modify themselves throughout their lifetime producing ontogenetic modifications, adaptations and variations. First, physical agencies and environmental influences may induce modifications in organisms (mechanical). Second, there are spontaneous activities such as "rising to the occasion" that can also result in modifications (nervous). Third, conscious agencies, such as intelligence, may also facilitate adaptation (intelligent). Intelligence, which includes learning, is a form of phenotypic plasticity, which enables animals to adapt to changing circumstances (e.g. changes in their ecological and social environment). Baldwin (1896) proposed that these adaptations, secured by organisms via intelligence, might influence genetic evolution. These adaptations thus tend to accelerate evolution, since the ability of animals to explore diverse possibilities in their lifetime can set the context for new selective pressures.

Environmentally affected phenotypes are often undermined as a major evolutionary process, due to their apparent lack of a genetic basis (but see Agrawal, 2001). Price (2006) outlined two ways in which phenotypic plasticity may influence genetic changes: First, plasticity may be crucial for the survival of populations that find themselves in a novel environment, and second, this plasticity may set the context for future selection pressures. The mechanism West-Eberhard (2003) proposed to explain the evolution of novel phenotypes was that of genetic accommodation. She proposed that novel phenotypes can be environmentally induced (as well as by mutation) followed by the genetic assimilation or accommodation of the novel trait or traits, which can occur in

the following stages (taken from Pigliucci et al., 2006, p. 2364): "(1) Trait origin: a mutation or environmental change causes the appearance of a developmental variant expressing a novel trait. (2) Phenotypic accommodation (i.e. a rearrangement of different aspects of the phenotype) to the new trait, made possible by the inherent, pre-existing, plasticity of the developmental system. (3) Initial spread of the new variant, facilitated by its recurrence in the population, if the initial change is environmental (in other words, one does not have to wait for a rare mutation to occur again before reaching relatively high frequency in the population), and (4) Genetic accommodation (i.e. fixation by allelic substitution) of the novel phenotype, as the result of standard selection."

Therefore, genetic differentiation and specialisation may follow from the exploitation of a new habitat, given that there are associated costs with maintaining plasticity (e.g. innovation can be associated with the evolution of larger brains: Lefebvre et al., 2001; Sol et al., 2007). However, some empirical evidence suggests that the prevalence of certain behaviours does not necessarily lead to a decline in plasticity (Price et al., 2003). This suggests that the ability of an organism to respond to change is critical for their survival in heterogeneous or novel environments (Price et al., 2003), which in turn may be critical for the evolution and co-existence of different species.

3.3.3 Behaviour as an active participant in evolutionary change

In the past one and a half decades, many scientists have become more interested in the capacity of a given genotype to express several alternative phenotypes depending on the context. Only recently has phenotypic plasticity gained respect in evolutionary biology, in which the conventional notion of the genotype as a 'blueprint' for a single fixed outcome, has been replaced by a more fluid concept of 'environmentally contingent phenotypic possibilities', technically known as 'norm of reaction' (Sultan, 2000). Future studies, however, need to focus on the exact mechanisms of phenotypic plasticity and the costs and benefits of plasticity in different environments, and the nature of these costs and benefits to understand why some animals are more plastic than others, and the environments in which phenotypic plasticity is favoured. Ideally, a new framework for understanding mechanisms of phenotypic plasticity should integrate our current knowledge of natural and sexual selection, since it is unlikely that these evolutionary

mechanisms are mutually exclusive. One important aspect of phenotypic plasticity, relevant to my thesis, is the active role of behaviour in the evolution of novel adaptations, in particular the way animals respond to competition that also enables co-existence with rival competitors. This is elegantly described in Hardy's book 'The Living Stream' (taken from Bateson, 2004):

It is adaptations which are due to the animal's behaviour, to its restless exploration of its surroundings, to its initiative in seeking new sources of food when its normal supply fails or becomes scarce through competition, that distinguish the main diverging lines of evolution; it is these dynamic qualities which lead to the different roles of life that open up to a newly emerging group of animals in that phase of their expansion technically known as adaptive radiation. What are the main features that do in fact distinguish the different diverging lines of evolution to be found both in the outbursts of the reptiles in the mesozoic age and of the mammals in the tertiary period? They are behavioural differences associated with their newly exploited environments; the development of new habits giving us the lines of runners, climbers, burrowers, swimmers and conquerors of the air. It cannot have been a new mutation or reassortment of genes that made an animal long used to terrestrial life begin to take to the water for its food. Again and again in the long history of the terrestrial vertebrates we have seen different forms, particularly among reptiles and mammals, but also, of course, among birds (and the more terrestrial lines of amphibia) turning to the water for their food. Some, of course, have become completely aquatic like the extinct Icthyosaurus and modern whales which show such a wonderful convergence in evolution between reptiles and mammals, towards a fish-like form.

Hardy 1965: 192–193

Hardy emphasised the importance of exploration (i.e. flexibility) for identifying novel possibilities and solutions to increasing competition over resources. By interpreting the individual as an active participant in the evolutionary process, we can understand why the predictions of the "Population Principle" developed by Thomas Malthus (1798) were false. Malthus predicted a drastic decrease in human population growth, caused by famine, war, disease etc., as competition over limited food supplies increases. Malthus,

however, failed to recognise the full complexity of human behaviour, i.e. our ability to adapt, for example through our technological advances, to changing circumstances.

The active role of behavioural innovation and flexibility in evolutionary processes is supported in birds by a recent phylogenetic comparative study on 3556 species of Parvorder Passerida. This study revealed that differences in behavioural flexibility among the different taxa are linked to differences in species richness. For example, species rich taxa (Passerida, Corvida, Psittaciformes, Accipitrida and Ciconiida) show rapid adjustment in their feeding behaviour or foraging techniques (Nicolakakis et al., 2003). They concluded that behavioural innovation alongside social transmission of a novel 'trait' to other members of the population might result in rapid evolution and thus species richness.

Behavioural flexibility may solve the paradox I addressed at the beginning of this section: Why are competitively 'inferior' individuals not eliminated from populations? The solution to this is reflected in the flexible behaviour of animals that can change instantly in response to novel environmental or social situations. Plasticity or flexibility in behaviour can sustain animals in the population even when they have a low competitive ability. For example, cheetahs are able to co-exist with their primary competitors, hyenas and lions, despite being competitively 'inferior' (Durant, 1998). It was initially supposed that interspecific competition must be negligible compared to intraspecific competition in order to sustain the coexistence of diverse species (see Durant, 1998). However, as we have seen in the case of spotted hyenas and lions, that interspecies competition can be severe. Many studies on interspecific competition have demonstrated the importance of spatial heterogeneity for maintaining co-existence of predator-prey interactions, but similar studies in competitive situations (e.g. predator-predator interactions) are rare (see Durant, 1998). Therefore, Durant (1998) investigated how cheetahs maintain themselves in ecosystems with their main competitors, which are responsible for their low densities (Laurenson, 1995) and high cub mortality rates (Laurenson, 1994). Durant (1998) demonstrated that cheetahs were found in lower density prey areas compared to their main competitors, and were able to avoid superior competitors facultatively (depending on the density of rivals and the intensity of the competition for food), by seeking out spatial and temporal refuges. Thus, Durant (1998)

concluded that the combination of mobility in cheetahs and spatial heterogeneity, promotes their coexistence.

3.3.4 Phenotypic plasticity and context-dependent sexual behaviour

Finally, phenotypic plasticity should also be applied to the way we investigate male and female mating behaviour, rather than pre-assuming sex-specific gender roles, e.g. choosy females vs. eager undiscriminating males (Gowaty and Hubbell, 2005). Gowaty and Hubbell (2005) proposed that the occurrence of choosy vs. indiscriminate mating behaviours depends on the time available for mating and the fitness differences between potential mates. Thus, according to this hypothesis, selection favours the flexible expression of choosy, indiscriminate and competitive mating behaviour, which is induced by time-varying life histories, environmental and social cues.

According to this model of adaptable and flexible sex role behaviour (termed DYNAMITE), the sexes do not behave according to any fixed sex roles, but instead first assess the fitness outcomes of adopting a choosy vs. indiscriminate behaviour (e.g. *Calopteryx haemorrhoidalis,* Córdoba-Aguilar et al., 2003). Thus, it is expected that the sexes can change their behaviour at any time to fit dynamically changing circumstances. Therefore, choosy behaviour in males and indiscriminate mating by females can also occur if favoured by the circumstances (e.g. if females have longer dormant periods before becoming sexually active again). Also, choosy behaviour in females does not necessarily imply indiscriminate behaviours in males (or vice versa). Finally, Gowaty and Hubbell (2005) addressed the question of 'why the sexes are how they are', regarding "sex typical behaviour" of choosy and indiscriminate mating behaviours? They suggest, that to really understand how different the sexes really are, we need to determine whether between-sex variation is larger than within-sex variation in the assumed 'sex-typical' behaviours. If it is indeed the other way round, then we need to re-think whether sex-roles do in fact exist. Are the typical differences in mating behaviour between the sexes genetically influenced, or do ecological factors shape the behaviours adopted by each sex? Or both? (Gowaty and Hubbell, 2005). To answer these interesting questions, Gowaty and Hubbell (2005, p. 943) proposed that the levelling of ecological contexts of males and females under controlled conditions is necessary. Thus they concluded that:

"If the ecological theatres in which the sexes play are different and if different ecological theatres account for sex differentiated behaviour, the question will become: what makes for ecological and social differences experienced by individual males and females?"

4. Conclusions

In conclusion, ideas and studies on phenotypic plasticity are a step towards understanding the diversity of animal behaviour, their life histories and population dynamics. For example, researchers are now becoming increasingly interested in the study of behaviour as an active participant in generating novel evolutionary possibilities of change and adaptation (e.g. see Bateson, 2004). Given that behaviour can influence an organism's fitness, competition does not necessarily lead to the elimination of 'unfit' individuals as long as they are likely to adjust to their local (individual) and non-local (environmental) circumstances.

This, along with the appreciation that the 'fittingness' of individuals can change depending on their own unique responses to competition, which in turn may lead to shifts in selective pressures, may help to dissolve some inconsistencies in our logic (e.g. the lek paradox: see Chapter 1). For example, in odonates environmental effects on male phenotype can be greater than effects resulting from genetic variation underlying those traits (Fincke 1997), which, according to the gene-centric approach (see Dawkins, 1976), would constrain the advantage of direct female choice. However, when genetic accommodation is taken into account, this phenomenon not only can be understood as an advantage to female choice, but also gives female choice an active role for influencing the degree and direction of evolutionary change in male traits. Therefore, phenotypic plasticity may be the key to understanding phenotypic diversity, since it does not invoke an absolute definition of fitness, but instead a more fluid concept of 'fittingness', which stresses the fit between an ever dynamically changing organism and environment.

Also, assuming that phenotypic plasticity and genetic diversity are closely associated, we can explore how animals respond to competition in a way that enhances their own

fitness by maintaining, rather than eliminating, diversity (since diversity and flexibility promotes phenotypic plasticity and vice versa). Thus, I propose that competition may provide the necessary creative 'tension' between individuals that allows for the evolution of novel adaptations, which depending on context may lead to the differentiation either within or between the sexes. Conversely, ecological competition, unpredictable resource abundance or threat of predation may also promote integration (i.e. the evolution of sociality and cooperation). Also, these adaptations may lead to a reduction in competition, thus enabling the co-existence of diversity both within and between species. Finally, an appreciation of both male and female perspectives and relatively novel ideas in evolutionary biology such as behavioural plasticity/flexibility is crucial for understanding adaptive responses to competition, especially when attempting to integrate diverse studies on intraspecific competition into a coherent framework.

5. Future directions

With the increasing popularity of phenotypic plasticity and the active role of behaviour in evolution, I am left with a strong impression that the field of evolution is undergoing a shift in perspective. Although new ideas and perspectives always need to be supported by scientific investigations, I believe that science can only benefit from an integrative approach to the study of evolution and behaviour. I suggest that acknowledging that organisms are distinct, but not discrete can complement much of our current scientific understanding of evolutionary processes. By viewing organisms as distinct, in which independence is always a matter of degree, we can investigate different scales of organisation from the relationships between the genotype and phenotype, and organism and society without assuming *a priori* that there is a conflict of interest between these diverse scales. This is no more of an assumption than the claim that individuals *are* discrete objects. However, the neo-Darwinian logic of competition relies on the latter assumption, because natural selection can only act on discrete sets of genes. However, new approaches to evolution such as genetic accommodation do not depend on discreteness, since the flexibility of behaviour can in turn affect animal relationships, which can influence novel evolutionary directions.

To conclude, the core of my argument in this thesis is based on the recognition and demonstration that animals can respond adaptively to their dynamically changing

context. Also, I have discussed feminist arguments in biology, which have exposed the inconsistencies that can arise when the sexes are stereotyped as having specific sex roles. I studied competitive relationships in diverse animal taxa, including birds, insects and mammals. These individual studies address different contexts of competition and how they are related to diverse behavioural and/or morphological adaptations. In bustards and American rubyspot damselflies I showed that competition over mating is related to different mating behaviours. In bustards SSD is related to the intensity of competition and display type, while in the American rubyspot condition appears to influence the mating tactic adopted by males. In spotted hyenas on the other hand, I focused mainly on competition between females in the dominance hierarchy, rather than mating behaviour, because female social rank appears to be the most important determinant of reproductive success and offspring survival. This emphasises that animals invest in reproduction in a way that maximises their fitness depending on physiological (e.g. energetic reserves), social, ecological and life history factors.

Competition and dynamically changing contexts thus result in diverse context-dependent behavioural adaptations, which I believe may play a critical role in directing novel selective pressures. In this scenario, individual differences resulting from phenotypic/behavioural plasticity enable animals to adapt to changing and unpredictable environments. Furthermore, phenotypic plasticity can at least partially explain how fitness gradients are created and maintained in natural populations, since animals that learn how to adapt to their surroundings throughout their lifetime can enhance their chances of survival and reproduction. Therefore, depending on the adaptability of novel behavioural traits, selection can potentially favour a diverse range of phenotypes. Thus, the role of competition in a social and environmental setting is viewed as a potentially creative process, rather than an eliminative process. The role of phenotypic plasticity in evolution requires much further exploration. However, I hope I have succeeded to interest the readers in the flexibility of animal behaviour and the exiting new areas of research it has to offer.

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Appendix

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The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae)

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Bustards vary considerably in sexual size dimorphism (SSD), ranging from reversed-dimorphic species (i.e. male < female) through monomorphic species to species in which an adult male can be three times heavier than an adult female. We used this unusual interspecific variation to test functional hypotheses of SSD using phylogenetic comparative methods. We found a strong allometric relation between SSD and body size that is consistent with Rensch's rule. We then tested whether the intensity of mating competition and the agility of male displays relate to SSD. First, the intensity of mating competition hypothesis predicts that males should be larger than females in species in which the males compete intensely for mates. As predicted, evolutionary changes towards more polygynous mating systems in bustards were associated with relatively larger males. Second, our results are also consistent with the aerial agility hypothesis, since in agile bustards the males tend to be smaller than females, whereas in nonagile bustards the males are usually larger. We also found that these two types of sexual selection have independent and statistically significant influences on SSD. We conclude that SSD in bustards is most consistent with sexual selection, and is influenced by both the intensity of sexual selection and the agility of male displays. Other hypotheses, however, such as fertility selection acting on females and differential use of niches by males and females remain untested.

Sexual size dimorphism (SSD) is one of the most conspicuous differences between the sexes. Several functional hypotheses have been proposed to explain SSD (reviewed in Hedrick & Temeles 1989; Shine 1989; Andersson 1994). First, directional selection may act on males (or on females). Sexual selection via male–male competition or female choice favours large male size in several birds and mammals (Webster 1992; Mitani et al. 1996; Dunn et al. 2001; McElligott et al. 2001; Lindenfors et al. 2003). Thus, an increase in body size may be particularly advantageous to males in polygynous species (Clutton-Brock & Harvey 1977; Owens & Hartley 1998), in which the intensity of sexual selection is greater because of increased competition between males over females.

Second, the direction of sexual selection on body size may also depend on whether the contest takes place on the ground or in the air (Payne 1984; Jehl & Murray 1986; Figuerola 1999). For example, small and agile males may have an advantage in contests that take place in the air (Andersson & Norberg 1981), and females also prefer small acrobatic males to large (or less acrobatic) males in raptors and shorebirds (Grønstøl 1996; Hakkarainen et al. 1996; Blomqvist et al. 1997; Figuerola 1999).

Third, disruptive selection may influence the body sizes of males and females towards different evolutionary optima. For instance, if males and females compete for resources, then each sex may benefit from avoiding extensive overlap with the other ('different niche utilization', Selander 1966; Shine 1989; Thom et al. 2004). However, it is difficult to distinguish whether differential niche

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utilization is a cause or a consequence of SSD. Thus, the exploitation of different resources may help maintain SSD, although it is unlikely to be the driving force behind it (Thom et al. 2004). Recent comparative studies have adopted a broad approach by investigating the influences of both sexual selection and ecological processes on SSD (Figuerola 1999; Székely et al. 2000; Perez-Barbería et al. 2002).

Many animal taxa show an allometric relation between body size and the extent of SSD across species (Rensch 1960). This relation, termed 'Rensch's rule' (Abouheif & Fairbairn 1997; Fairbairn 1997), states that among closely related taxa SSD increases with body size in those species in which the male is larger than the female, whereas SSD decreases with size in species in which the female is the larger sex. A recent genetic simulation model suggests that SSD may change rapidly in response to divergent selection pressures without significant long-term change in the genetic correlation between the sexes (Reeve & Fairbairn 2001).

Bustards (Otididae) are an excellent group with which to investigate SSD (Dale 1992), since they have one of the largest size dimorphisms in any avian taxa. In addition, they include species that have male-biased (e.g. great bustard, *Otis tarda*) and female-biased (e.g. lesser florican, *Sypheotides indicus*) dimorphism. Their mating behaviour ranges from socially monogamous to lek breeding. In the lek-breeding great bustard large males gain about 30% in body mass at the onset of the mating season, which suggests that large body mass enhances mating success (Carranza & Hidalgo-Trucios 1993), although it may also allow males to store reserves for the period of intensive displays. Male bustards also show an unusual range of display behaviour from spectacular ground displays by great bustards to highly acrobatic displays by red-crested bustards, *Lophotis ruficrista*. Finally, a recent molecular phylogeny provides a phylogenetic framework for comparative analyses (Pitra et al. 2002). Phylogenetic comparative methods are often used to test functional hypotheses of SSD (Owens & Hartley 1998; Székely et al. 2000; Dunn et al. 2001). These methods are useful for comparing traits across species or taxa within a statistical framework that controls for the effects of common ancestry.

We had two objectives in this study: first, to test whether SSD relates to body size in bustards as expected from Rensch's rule and second, to test two mutually nonexclusive functional hypotheses of SSD. The intensity of mating competition hypothesis predicts that males should be larger than females in species in which males compete intensely for mates, whereas the display agility hypothesis predicts that males should be relatively smaller than females in species with aerial displays compared with species with nonagile male displays, since reduced body size is assumed to enhance agility.

METHODS

Data and Phylogeny

We compiled data on body size, mating behaviour and male agility from primary research publications, handbooks and unpublished information (Appendix 1). Social mating system, a proxy for the intensity of mating competition, was scored as monogamy, territorial polygyny and lek polygyny. We assumed that mating competition increases from monogamy (score 1) to lek polygyny (score 3, see similar scoring by Székely et al. 2000; Dunn et al. 2001). Three species showed both territorial polygyny and lekking, so were scored 2.5 (Appendix 1). Our scores were highly correlated with an independent scoring of mating system (Dale 1992; $r_S = 0.901$, $N = 17$ species, $P < 0.0001$). Male agility was scored between 1 (low) and 5 (high, Appendix 1). This scoring of male agility is consistent with the approach of Figuerola (1999) and Székely et al. (2000). The score of 1.5 was given when it was uncertain whether male display was 1 or 2 (Appendix 1). The distinctions between scores 1, 1.5 and 2 are ambiguous, so we took the advice of an anonymous referee and combined these scores in the analyses. Note that using the original scores (Appendix 1) does not change our major conclusions.

Initially, we attempted to collect data on body mass of bustards as a further proxy for body size. Mass data, however, are subject to daily and seasonal fluctuations (Carranza & Hidalgo-Trucios 1993; Witter & Cuthill 1993). In addition, sex-specific mass data were available for only a few species. We therefore omitted body mass from the analysis.

The bustard phylogeny was provided by a recent molecular study (Pitra et al. 2002) that used sequences from the mitochondrial cytochrome *b* gene, the noncoding mitochondrial control region II and an intron–exon crossing fragment of the nuclear chromo-helicase-DNA binding gene. We augmented this phylogeny with two species (Karoo bustard, *Eupodotis vigorsii*, and the little brown bustard, *Eupodotis humilis*). The phylogenetic position of the latter two species was provisionally allocated as sister taxa to Rüppell's bustard, *Eupodotis ruepellii*, because both the Karoo bustard and the little brown bustard were formerly placed in a separate genus (*Heterotetrax*) together with Rüppell's bustard (Snow 1978).

Phylogenetic Comparative Analyses

We used the phylogenetic independent contrasts method of Felsenstein (1985) as implemented by CAIC (Purvis & Rambaut 1995) to control for phylogenetic nonindependence of species. Wing length (mm) was log transformed prior to the analyses. An assumption of Felsenstein's method is that standardized contrasts should be independent from their estimated nodal values. We verified this assumption by plotting standardized contrasts against the estimated nodal values for our variables: none of these correlations were statistically significant.

We tested the allometric relation between male and female body size by fitting major axis regressions (Sokal & Rohlf 1981) using either the species data or the phylogenetic independent contrasts (Garland et al. 1992). Rensch's rule predicts that the slope of male:female size should be significantly larger than 1. The major axis regression of phylogenetic independent contrasts was forced

through the origin (Harvey & Pagel 1991). We provide the slope of major axis regressions (b) and the 99% confidence intervals (lower CI–upper CI) that were calculated by bootstrapping the contrasts.

We calculated SSD as contrasts in log (male wing) − contrasts in log (female wing). It is customary to use log-transformed data for calculating SSD since the differences between males and females expressed as logarithms provide more accurate estimates of SSD than ratios do. Log transformation of sizes also makes the more reasonable assumption that different lineages are equally likely to make the same proportional change in size (Purvis & Rambaut 1995). Least-squares regressions of contrasts were forced through the origin, because the model predicts the mean value of independent contrasts to be zero (Harvey & Pagel 1991). We investigated the relations between SSD (dependent variable), the intensity of mating competition and male agility (independent variables) in bivariate and multivariate least-squares regressions. Evolutionary changes in agility and the intensity of mating competition were not related (Pearson correlation: $r_{24} = 0.136$, $P = 0.516$). We also tested the interaction term between the intensity of sexual selection and male agility (with SSD as the dependent variable). This interaction was not significant ($N = 24$ contrasts, $P = 0.484$), so we excluded the interaction term from the final multivariate regression model. In the multivariate model we provide the partial correlation coefficient r_p, the significance of r_p and effect sizes (partial η^2). We used SPSS version 11.00 (SPSS Inc., Chicago, IL, U.S.A.) for statistical calculations, except that bootstrapping of confidence intervals for major axis regression was carried out in R (Ihaka & Gentleman 1996).

RESULTS

Rensch's Rule

Our results are consistent with Rensch's rule since male-biased SSD was greater in large bustards than in small ones, and the 99% confidence intervals did not include 1 (Fig. 1a). These results remained statistically significant when we used phylogenetically independent contrasts (Fig. 1b).

Intensity of Mating Competition and Male Agility

Evolutionary changes in SSD were positively correlated with changes in the intensity of mating competition (Fig. 2a). Since the contrasts were highly variable around zero, we repeated the analysis by excluding zero contrasts (see a similar approach by Owens & Hartley 1998). Nevertheless, the relation remained significant ($r = 0.645$, $F_{1,9} = 6.395$, $P = 0.032$).

Evolutionary changes towards agile displays were also correlated with changes towards smaller males relative to females (Fig. 2b). The strength of the relation remained after we excluded zero contrasts, although it was not statistically significant ($r = -0.424$, $F_{1,11} = 2.413$, $P = 0.149$).

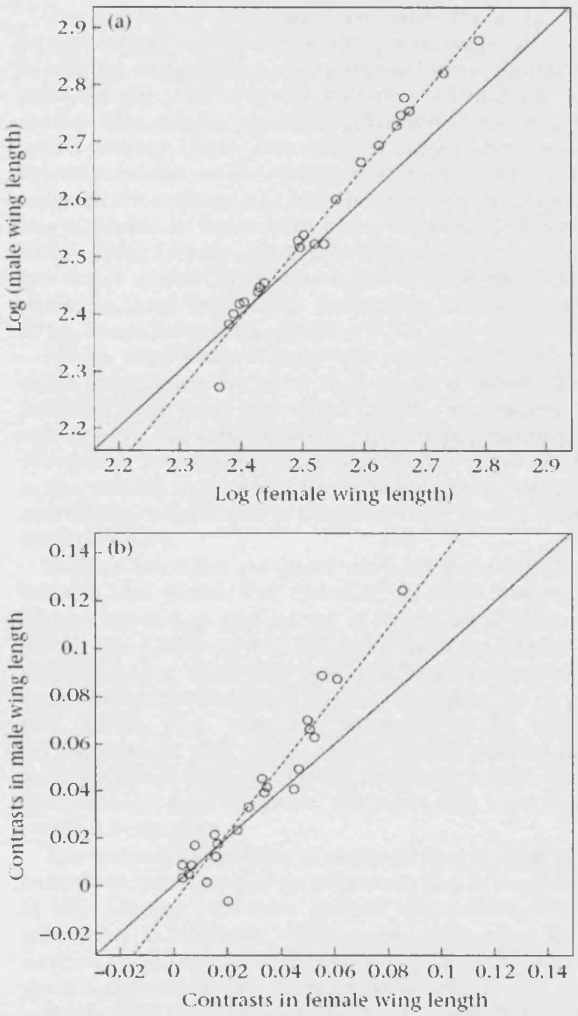

Figure 1. Rensch's rule in bustards. The continuous line indicates the isometric relation and the dotted line represents the fitted relation between male size and female size by major axis regression for (a) species ($b = 1.311$, 99% confidence intervals 1.204–1.430, $N = 25$ species) and (b) phylogenetic contrasts ($b = 1.542$, 99% confidence intervals 1.218–1.846, $N = 24$ contrasts).

In the multivariate model ($r^2 = 0.431$, $F_{2,22} = 8.342$, $P = 0.002$), both the intensity of mating competition and male agility were associated with SSD. Evolutionary changes towards larger males relative to females were associated with both intensified mating competition ($r_p = 0.563$, $F_{1,22} = 10.197$, $P = 0.004$) and reduced agility of male displays ($r_p = -0.533$, $F_{1,22} = 8.749$, $P = 0.007$). Effect sizes of mating competition and display behaviour were partial $\eta^2 = 0.317$ and 0.285, respectively.

DISCUSSION

Our study confirms Rensch's rule in bustards (Payne 1984), and adds to a growing number of taxa in which the rule has been shown, including mites, lizards,

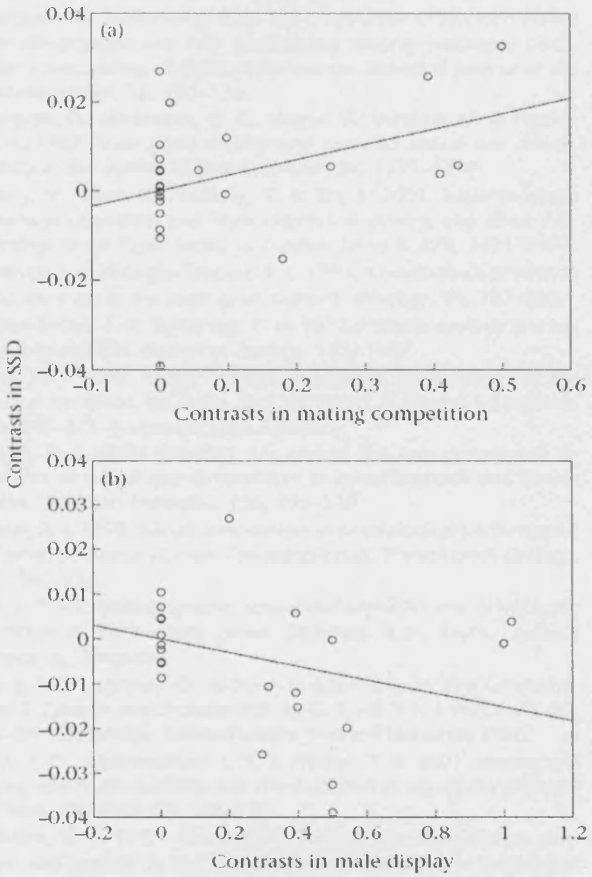

Figure 2. Phylogenetically independent contrasts in sexual size dimorphism (SSD) and (a) the intensity of mating competition ($r = 0.453$, $F_{1,23} = 5.934$, $P = 0.023$) and (b) male agility ($r = -0.409$, $F_{1,23} = 4.634$, $P = 0.042$). Regressions were forced through the origin.

hummingbirds and shorebirds (Abouheif & Fairbairn 1997; Cullum 1998; Colwell 2000; Székely et al. 2004). Székely et al. (2004) have shown that the rule is driven by the interaction between mating competition and male display behaviour in shorebirds. In bustards, however, this interaction was not significant ($P = 0.484$). We suggest that the latter result may be caused by the small number of bustard species in the analysis, which limits the statistical power of models. Note, however, that the predictive power of multivariate models was comparable between bustards ($r^2 = 0.431$) and shorebirds ($r^2 = 0.476$–0.454, Székely et al. 2004).

The relation between mating competition and SSD is consistent with the hypothesis that sexual selection is responsible for the large body size in males of polygynous species. This relation has been reported in New World blackbirds (Icteridae), shorebirds (Charadrii) and a wide range of other avian taxa (Webster 1992; Székely et al. 2000; Dunn et al. 2001). Thus, male–male competition and female choice may lead to an evolutionary increase in overall body size. Fertility selection is unlikely to explain SSD given that most bustard species lay only small clutches of one or two eggs (Collar 1996).

Our results are also consistent with the aerial agility hypothesis. The influence of agility was comparable to that of mating competition, as indicated by the partial effect sizes. Sexual selection will favour small males in those species that display aerially (Andersson & Norberg 1981; Jehl & Murray 1986). This relation has also been reported in nonpolyandrous shorebirds with reversed SSD, showing a significant reduction in male body size from species with less acrobatic to those with more acrobatic displays (Figuerola 1999; Székely et al. 2000). Evidence that females prefer small males also exists for moorhens, *Gallinula chloropus*, and fruit flies, *Drosophila subobscura* (Petrie 1983; Steele & Partridge 1988).

Future work may expand our study by investigating other morphological traits that relate to body size, for instance body mass and tarsus length. In addition, body size appears to vary between bustard populations, thus comparing populations may be a fruitful approach. Work is also needed to quantify the ecology, mating behaviours and display behaviours of bustards, most species of which are threatened.

Various selection pressures may act on body sizes of females and males. For instance, in most bustards the incubation of eggs and rearing of young are left entirely to the female (Collar 1996). This may select for smaller body size in females, since they would be better covered by vegetation during incubation and less conspicuous to predators. Large size, however, may allow the sexes to accumulate fat and buffer them against fluctuations in food resources. Thus, if one sex forages in a more variable environment than the other, the sexes may have different optimal body sizes.

The colours and pattern of plumage may amplify display behaviour, and thus play an important part in the evolution of SSD. Display behaviour appears to correlate with male coloration in bustards, since species with aerial displays have more melanin in their plumage (Dale 2006). The latter result is consistent with the findings of Bókony et al. (2003), who showed that more melanistic shorebirds have more agile displays. Thus, a further implication of aerial displays in males is that their plumage is more conspicuous against the light background of the sky.

In conclusion, our study shows that SSD in bustards is consistent with Rensch's rule. Our results also support the sexual selection hypothesis that directional selection may either increase or decrease body size of males, depending on the particular mating strategy and display type.

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Appendix 1

Table A1. Data sources

Species	Male wing (mm)	Female wing (mm)	Mating system	Display type	Source
Afrotis afra	281.0 (47)	270.0 (23)	PG	4	4
Afrotis afraoides	285.6 (18)	274.5 (13)	PG	5	1
Ardeotis arabs	604.0 (7)	496.7 (6)	PG	2	1
Ardeotis australis	569.0 (6)	474.0 (12)	PG	2	3
Ardeotis kori	758.0 (36)	616.0 (46)	PG	2	5
Ardeotis nigriceps	661.2 (12)	539.5 (11)	PG	2	1
Chlamydotis undulata	399.2 (25)	359.2 (26)	PG	3	1
Eupodotis caerulescens	333.5 (8)	330.8 (4)	MG	1	1
Eupodotis humilis	252.6 (10)	245.1 (8)	MG	1	1
Eupodotis rueppellii	329.0 (18)	313.0 (13)	MG	1	4
Eupodotis senegalensis	276.1 (14)	268.5 (4)	MG	1	1
Eupodotis vigorsii	337.4 (5)	312.3 (7)	MG	1	1
Houbaropsis bengalensis	333.0 (15)	343.4 (14)	PG	4	1
Lissotis hartlaubii	337.8 (10)	310.8 (6)	PG/LEK	1	1
Lissotis melanogaster	345.5 (26)	319.3 (23)	PG/LEK	4	1
Lophotis gindiana	262.8 (18)	250.1 (12)	PG	5	1
Lophotis ruficrista	263.9 (12)	254.5 (11)	PG	5	1
Lophotis savilei	243.0 (9)	240.8 (4)	PG	5	1
Neotis denhami	558.0 (11)	459.0 (7)	PG/LEK	2	5
Neotis heuglinii	495.0 (3)	423.0 (4)	PG	1.5	2
Neotis ludwigii	536.0 (6)	452.0 (5)	PG	1	4
Neotis nuba	463.5 (2)	395.0 (4)	PG	1.5	4
Otis tarda	600.1 (12)	464.8 (10)	LEK	2	1
Sypheotides indicus	187.8 (12)	231.7 (11)	PG	5	1
Tetrax tetrax	252.0 (29)	249.0 (15)	PG	4	2

The numbers of individuals (males and females) measured for each species are given in parentheses. Mean wing lengths were calculated from the unpublished measurements of P. Goriup and P. Osborne, where indicated. Social mating system and display behaviour were scored by P. G. from unpublished notes and observations. Mating system was scored as monogamy (MG), territorial polygyny (PG) and lek polygyny (LEK). Display type was scored as (1) ground display with vocalization only and/or erect neck display; (2) ground display; males inflate their oesophagus and reveal the underparts of the plumage; (3) ground display with running and occasional leaps in the air; (4) aerial nonacrobatic display of high flying; (5) aerial acrobatic rocket display (Johnsgard 1991). Note that display scores 1, 1.5 and 2 were combined in statistical analyses (see Methods). Source: (1) P. D. Goriup & P. E. Osborne (data compilers); (2) Johnsgard 1991; (3) Marchant & Higgins 1993; (4) Urban et al. 1986; (5) Percy FitzPatrick Institute of African Ornithology: http://web.uct.ac.za/depts/fitzpatrick/docs/fam31.html.